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Endogenous Plant Growth Promoters and Inhibitors in the Regulation of Rest in the Floral Bud, Vegetative Bud, and Seed of Prunus Persica.

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ENDOGENOUS PLANT GROWTH PROMOTERS AND INHIBITORS IN THE REGULATION OF REST IN THE FLORAL BUD, VEGETATIVE BUD, AND SEED OF *PRUNUS PERSICA*

A Dissertation

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in

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by
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ABSTRACT

Most investigations of the regulation of the rest period in peach utilized floral buds. Results implied that a promoter/inhibitor balance was involved. High levels of an inhibitor were found in late autumn and winter, while bud break in spring was correlated with low inhibitor levels and high levels of a promoter.

The present studies were conducted to determine whether activity of the vegetative buds and seed of peach was regulated by a similar mechanism as that implied for floral buds.

The floral and vegetative buds, from excised twigs, and seeds, after 0, 10, 20, 30, and 40 days of continuous chilling at 7.2 C were ether-extracted and fractionated into an acidic and a neutral/basic fraction, which were then partitioned by paper chromatography, using n-butanol:ammonia:water (10:1:1) as solvent, before being bioassayed for growth promoters and inhibitors using the wheat coleoptile straight growth method.

The results of the bioassays were plotted as histograms of coleoptile extensions, expressed as % of the controls, against 10 Rf values along the x axis. Conclusions derived were based on interpretations of the histograms and statistical analysis of the data.

Chromatographs of the acidic fraction of floral and vegetative buds had a zone of promotion at Rf 0.1-0.2, probably due to indolepyruvic acid and indoleacetic acid. Promoters at Rf 0.7 could be due

to indole acetonitrile and indole ethyl acetate. Inhibitive zones were found at Rf 0.4-0.6 and Rf 0.8-0.9, probably consisting of naringenin and/or abscisic acid. Chromatographs of the neutral/basic fraction had a zone of promotion at Rf 0.1, which was of an unknown nature. An inhibitive zone at Rf 0.4-0.9 could probably be composed of phenolic acids.

Chromatographs of the acidic fraction of unchilled seeds had a promotive zone at Rf 0.1, followed by an inhibitive zone at Rf 0.2-1.0. The inhibitor decreased upon chilling up to 30 days, then increased to original levels after 40 days of chilling. The nature of the substances was not determined. There were no definite promotive zones in chromatographs of the neutral/basic fraction and presence of inhibitive zones was inconsistent.

Data obtained in this study did not suggest that a promoter/inhibitor balance was involved in the regulation of rest in peach buds. The results indicated that the rest period of the floral and vegetative buds could probably be regulated by the same mechanism involving identical substances. A proposal was made which could account for presence of high levels of inhibitors when rest was broken. The proposal was that abscisic acid, probably one of the many inhibitors found in the scales, responding to a "message", caused the formation of abscission layers in the scales, which thus reduced the influence of the inhibitors on the bud primordium to the extent that growth could occur if the environmental conditions were favorable. This proposal was based on observations that emerging buds have scales which could be easily detached along lines

of abscission, implying that abscission layers were laid down previously.

The seeds of peach probably have a different mechanism for the regulation of rest from that of the floral buds. The seed response to chilling differed from that of the floral buds, and the growth promoters and inhibitors did not appear to be similar, as they occurred at different Rf values in the chromatographs.

Results obtained from pecan buds indicated that they could have a mechanism for regulation of rest similar to that of peach buds. The emergence of pecan buds followed abscission of bud scales along a distinct line of abscission, and the chromatographs indicated presence of inhibitive zones in both the acidic and neutral/basic fractions which correspond to similar zones in peach.

INTRODUCTION

The floral and vegetative buds of peaches (Prunus persica L. Stokes) grown in locations with mild winters have often suffered from "prolonged dormancy".

According to one theory, the prolonged dormancy is due to insufficient chilling of the buds during the winter, with the result that they remain in a condition of rest.

Each peach cultivar has a specific chilling requirement needed to break the rest period. This requirement is expressed numerically by the total number of hours of temperature that is 7.2 C and below. Peach cultivars are commonly classified by their chilling requirements. Though an arbitrary means of expression, this method of classification still serves as a useful guide in determining the adaptability of a cultivar to a locality.

The discovery of growth promoters and growth inhibitors in plants has switched the emphasis from the external factors to the internal factors involved in the regulation of rest. The concept evolved is that the rest period is regulated by a balance between growth promoters and growth inhibitors. The onset of rest is due to an accumulation of growth inhibitors and if the plant has more "inhibition units" than "promotion units" then the plant remains at rest. When promotion units outnumber inhibition units, rest is completed and growth may occur if environmental conditions are favorable (96).

Nearly all of the studies of the mechanism of the regulation of rest in peach have utilized floral buds. This study sets out to determine whether the vegetative buds are controlled by the same mechanism of an inhibitor/promoter balance implied by investigations of floral buds.

The vegetative buds, when expanded, have essential roles to play in the production of a fruit crop in that they protect the blossoms from frost damage and the bark from sun scalding while at the same time they supply the plant with metabolites needed for growth and development.

Since there appear to be many similarities between bud dormancy and seed dormancy of peaches, this study will also examine whether or not the same mechanism regulates dormancy in these two organs.

It is hoped that the results of the study will contribute to a better understanding of the mechanism regulating rest in peach and will aid in the development of reliable practical means of controlling bud break.

REVIEW OF LITERATURE

Bud Dormancy

The study of bud dormancy in higher plants has attracted much interest for many years. It is now generally agreed that this phenomenon consists of three phases (99). At the pre-dormancy or summer dormancy phase, the bud is held in check by correlative inhibition where the influence arises from outside the bud, such as the inhibition of lateral buds by the subtending leaves or by the main apex in an active shoot (85).

The second phase in bud dormancy is characterized by the inability of the bud to grow when correlative inhibition is removed or under external conditions which at other phases are quite favorable for active growth. The terms true dormancy, deep dormancy, winter dormancy, and rest are used synonymously for this middle phase.

After an appropriate period of rest the bud is capable, at the latter part of winter or early spring, of growth but is held back by unfavorable environmental conditions, particularly temperature. This last phase is referred to as post-dormancy, or after-rest.

This study deals with the true dormancy or rest phase. The terms "dormancy" and "rest" will be used interchangeably.

Many theories have been proposed concerning the mechanism involved in the regulation of rest. Earlier workers stressed the importance of mechanical barriers, such as bud scales, to the free

flow of oxygen and the products of anaerobiosis (25, 27, 28, 29). Vegis (94) in 1964 re-emphasized this theory.

A second theory is based on the concept that rest is regulated by a balance between growth promoters and inhibitors in the organs concerned (73, 75, 101).

A very recent theory postulated that rest is controlled at the molecular level by gene activity and involves the repression and derepression of deoxyribonucleic acid (DNA) (12).

This study deals with the roles of plant growth promoters and inhibitors in the regulation of rest in the peach. The review will thus deal mainly with those aspects pertaining to this thesis.

Chilling Requirement of the Peach

Because of the commercial importance of peach, the rest period in its buds, especially the floral bud, has attracted much interest for many years. According to the older theory, the rest period of a cultivar is regulated by the amount of chilling it receives over the winter months. Insufficient chilling to meet the chilling requirement results in prolonged rest and erratic bud break in spring. This concept of a cold requirement to break rest was originally proposed by Coville in 1920 (24). The cold requirement is expressed numerically by the total number of hours of temperature that is 7.2 C (arbitrarily set) and below which has been accumulated by the bud over the cold period. Listings of popular cultivars of peaches, together with their chilling requirements were commonly published. Weinberger (105) listed 65 cultivars with a range of 750 hours for cultivars with a low chilling requirement to 1150 hours for those

that required more chilling. Chandler et al. (18) and Yarnell (110) quoted figures that ranged from 800 to 1400 hours. For the same cultivar different workers have established different chilling requirements. This is due as much to the methods used in the derivation as to the location and the multitude of environmental and edaphic factors involved in the cold requirement of a cultivar. Chandler et al. (18), Yarnell (110), Brooks and Philp (14), Lammerts (60), Lesley (61), and Weinberger (105) have used different criteria for the establishment of the chilling requirement. Generally vegetative buds of a cultivar require slightly more chilling than floral buds, usually some 50 to 100 hours more. Breeding programs have had chilling requirement as an important factor (60, 61).

Growth Regulators and the Rest Period

Concurrently, after the discovery of auxins by Went (108), there was a growing realization that growth promoting substances may be involved in the regulation of rest.

The approaches adopted in the study of this relationship involved either attempts to show correlation between levels of endogenous growth promoters and the state of dormancy of the bud, or the application of exogenous growth promoters to terminate rest. Attempts to show the former have not been too successful (7, 64, 87, 104). The latter approach resulted in opposing mechanisms being proposed (6, 34).

Bennett and Skoog (6) in 1938 applied various growth promoting compounds or their precursors to peach trees in order to break the rest. They found that tryptophane, an auxin precursor, and vitamin B_1 gave weak growth. Slightly stronger growth was obtained when

heteroauxin (β-indole-acetic acid) was used. The best growth was obtained with brewer's and baker's yeast. They postulated that as a result of exposure to low temperature a precursor of auxin accumulated in the bud followed by a gradual appearance of the "free" or "diffusible" auxin. This appearance of the auxin in the bud was correlated with the ending of rest. On the other hand Eggert (34), working with apple buds, came to the conclusion that a critical level of the total auxin concentration existed in the buds. If the total auxin concentration of the buds was above the critical level, growth was inhibited and the buds were in rest. When the total auxin concentration was below the critical level growth was possible, indicating the end of rest. The absolute values of this critical level varied with species and the cultivar. Mitchell and Cullinan (68) applied different amounts of different growth promoters to peach twigs and obtained varyir success depending on dosage used, cultivar of peach and time of application.

The discovery by Hemberg (45, 46) of an inhibitor in the dormant buds of potato set investigators in a new direction which ultimately resulted in the current concept that a balance of growth promoters and inhibitors regulates the rest period. He observed that there was a correlation between the state of dormancy and the levels of the inhibitor in the buds of the potato and the buds of Fraxinus excelsior (47).

Blommaert (9, 10) in South Africa, was one of the first to report the presence of growth promoters and an inhibitor in peach flower buds. He found that auxin activity was at a maximum when spring growth commenced. The inhibitor level decreased during the dormant period

and was completely absent when rest was broken. In the United States, Hendershott and Bailey (50) obtained similar results, though they could not explain a second peak of inhibitory activity just prior to bloom. Hendershott and Walker (51), working with the flower bud, found three growth promoters and one inhibitor in the dormant buds. The greatest quantity of growth promoters was found in the latter part of winter. The level of the inhibitor remained high over the winter but completely disappeared two weeks before bloom. The inhibitor was identified as a flavanoid, naringenin (52). Nevins and Hemphill (70) also reported the presence of three growth promoters, one less than the number reported by Blommaert (9). Dennis and Edgerton (30), working with peach flower buds in New York state concluded that the inhibitor level was related to the post-dormancy phase rather than with true dormancy. They found that the level of the inhibitor was high when rest was broken but was completely absent in the post-dormancy phase. Corgan (21) also found that the inhibitor did not disappear with the termination of rest, but was apparently diluted as buds swelled following rest. He reported that the concentration of naringenin in dormant flower buds varied from 0.44% to 1.7% of the fresh weight of the buds. The concentration at full bloom was 0.03%, whereas 0.01% naringenin in solution was sufficient to completely inhibit growth of wheat coleoptiles. To eliminate any dilution effects, El-Mansy and Walker (37) measured naringenin both on a weight basis and on a bud basis and found that naringenin content was much higher during rest than after the rest period was completed when observed on a per bud basis. The lowest value was observed just prior to bloom.

Gibberellic acid (GA) was added to the list of substances believed to be involved in the regulation of rest after it was reported by Rappaport (78) and Kahn et al. (53) that gibberellic acid could break the rest in potato tubers and lettuce seeds. Donoho and Walker (31, 97) and Hatch and Walker (44) found that they could break the rest of vegetative buds but not the floral buds of peach with the application of gibberellic acid. It could also break the rest of peach seeds (19, 31). Chailakhian et al. (16) found higher levels of gibberellin-like activity in peach buds following chilling. Phillips (73) reported that when he applied a mixed solution of naringenin and gibberellic acid to dormant peach buds, the removal of dormancy imposed by naringenin depended on the relative concentration of gibberellic acid in the applied solution.

The work of Wareing and his co-workers (8, 32, 33, 35, 74, 75, 95) studying dormancy in forest trees ultimately led to the isolation and characterization of an inhibitor "dormin" (80, 81) from the β-inhibitor of Bennet -Clark and Kefford (5). This inhibitory activity was found to increase under short day conditions. In many woody species the formation of resting buds and the onset of dormancy was promoted by short days (81, 100). Dormin was found to be identical to the abscission accelerating substance "abscisin II" (23), originally isolated from young cotton fruits by Addicott and his co-workers (1, 2, 72), and now known by the name of abscisic acid (ABA) (3). Since then this substance has been found in many plant species and a wide range of plant tissues and organs (66, 67), including peach leaves. Corgan and Peyton (22) have considered it to be involved in the regulation of rest in peach flower buds and it has been considered

by Lipe and Crane (63) to be responsible for rest in peach seeds. Ryugo (82) also found it to be present in the peach endocarp.

Interest in ABA in recent years has overshadowed the isolation of other inhibitors from plant tissues. From the β-inhibitor complex, Varga (93) found a number of phenolic substances including o- and p-coumaric acid and salicylic acid. Tomaszewski (92) reported that p-hydroxygenzoic acid and p-coumaric acids were found in 119 species of plants. Naringenin isolated from resting peach buds is also a phenolic substance. For a time phenolic growth inhibitors were held to play an important role in the regulation of rest (49). A current review by Kefeli and Kadyrov does not exclude this possibility (54). On the other hand, Rappaport et al. (11, 79) concluded that none of the phenolic substances isolated from the β-inhibitor complex were responsible for dormancy in potato tubers.

The successful use of exogenous ABA to promote rest (36, 63) and the use of gibberellins to break rest (31, 44, 53, 78) gave rise to the current concept that rest may be regulated by a balance between endogenous hormones of this nature. Experiments in which ABA and gibberellins were applied together in various concentrations to tree buds indicated that the growth-inhibitory effects of ABA could be overcome by increasing concentrations of gibberellins (29, 32, 36).

In nearly all the reports of the presence of inhibitors in plant tissues, the acidic fraction of the plant extract was used, but in a recent work on the lateral bud dormancy of Ribes nigrum, Tinklin and Schwabe (90) found inhibitors in the neutral and basic fractions of the extract as well. Peak inhibitory activity was found in early autumn, and inhibitor levels were reduced by low temperature treatments.

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The decline was seen in the acidic as well as in the neutral and basic fractions.

Seed Dormancy

There are many similarities between bud dormancy and certain forms of seed dormancy. In Betula pubescens, the dormancy in both the bud and seed could be overcome by chilling, by long photoperiod and by gibberellic acid (8, 100). There is the possibility that the physiological and biochemical bases for the regulation of dormancy would be similar in both organs. Rosaceous seeds have been known to require an after-ripening at low temperature before germination would take place. Crocker and Barton (26) found that mature Elberta peach seeds needed an after-ripening period of 14 weeks at 5 C. Carlson and Tukey (15) reported that depending on cultivars, the chilling requirements were from 2-3 weeks for those with a short after-ripening period to 10-12 weeks at 3-5 C for cultivars with longer after-ripening periods.

The removal of the seed coat has resulted in immediate germination of non-after-ripened seeds, but the seedlings obtained were dwarfed (39, 76). It was suggested that dwarfing was the result of some growth-inhibiting compounds carried over from the seed (40, 41, 42, 43).

The possible involvement of growth regulators in seed dormancy has been much studied. Luckwill (64) found a growth inhibitor in the seed coat of freshly harvested apple seeds. This inhibitor disappeared after after-ripening was completed. He also noted that growth promoting substances were found in the embryos of after-ripened seeds just before

germination. In the peach, Biggs (7) reported larger amounts of growth inhibitors in non-after-ripened embryos than in after-ripened ones, but the concentration of growth promoters did not change during chilling. Weaver and Hough (104) obtained a correlation between increasing auxin concentration and a corresponding decreasing inhibitor concentration with advancing peach embryo maturity, but Flemion and de Silva (41) reported that there was no direct relationship between dormancy and the growth promoting and inhibiting substances they extracted from peach seeds. Villiers and Wareing (95) reported that chilling resulted in the development of a growth promoter which was capable of overcoming the dormancy of unchilled embryos of Fraxinus excelsior. This suggested that there could be an interplay between growth promoters and inhibitors in regulating embryo dormancy. Lipe and Crane (63) reported that the inhibitor found in the peach integuments was ABA. The inhibitor disappeared by the sixth week of chilling after which time the seeds germinated. They also reported that ABA was antagonistic to gibberellic acid, and partially reversed the growth induced by indoleacetic acid. Ryugo (82) confirmed that the inhibitor in peach seed was ABA. He also found that sustained leaching for three days removed the inhibitor. Wong and Dennis (109) found no consistent decrease in ABA levels in the seed coat, cotyledon and embryo axis of peach seeds that were after-ripened compared with non-after-ripened seeds. Their conclusion was that there was no obvious correlation between a decrease in ABA level and an increase in germination during after-ripening.

With the peach, Weinberger (107) found that cytokinin could overcome dormancy only when the chilling requirement had been partially

satisfied. With the hazel (Corylus avellana), the inhibiting effect of ABA was partially overcome by gibberellic acid (13). With lettuce and barley, the effect of ABA could not be overcome by gibberellic acid, but it could be reversed with kinetin (58, 59).

It was found that exogenous ethylene would stimulate germination of clover seed (38). It was observed by Ketring and Morgan (56, 67) that nondormant cultivars of peanuts actively produced ethylene during germination, while dormant cultivars produced only low levels.

Thus from the time of the discovery of auxins to the present time, each new growth regulator discovered has been implicated in the regulation of rest, either by itself or interacting with others.

MATERIALS AND METHODS

This study consisted of:

I. Thirty sets of bioassays for growth promoters and inhibitors in floral buds, vegetative buds and seeds of two varieties of peach after 0, 10, 20, 30 and 40 days of chilling at 7.2 C.

II. A peach seed germination and seedling characteristics study.

III. Application of peach bud extracts in the paper chromatogram segments to peach twigs.

IV. A set of bioassays for growth promoters and inhibitors in pecan bud scales after 0 and 60 days of chilling at 7.2 C.

I. Materials

Seed

Two cultivars of peaches which fruit well under local conditions at Idlewild Research Station, Clinton, Louisiana, were selected to provide the seed material. The cultivars were LaGem and LaGold. The former has been estimated to require about 850 hours of chilling and the latter needs about 750 hours. Fruits of the two cultivars, from single trees, were harvested on the same day (29th June, 1971) when most of the fruits on the trees were ready for picking. The fruits were depulped and soaked over-night to remove the last traces of pulp. The seeds of each cultivar were divided into five equal lots, mixed with moist vermiculite in plastic bags and subjected

to 0, 10, 20, 30 and 40 days of chilling at 7.2 C in a refrigerated room. Materials not immediately used for extraction were stored at -20 C.

Floral and Vegetative Buds

Twigs bearing floral and vegetative buds, from single trees, were harvested on September 23, 1971, when the buds were in rest. This was indicated by the failure of distal buds to break when the terminal bud and subtending lateral leaves were removed. The twigs were brought back to the laboratory as rapidly as possible and subjected to treatment. The leaves were removed before the twigs were subjected to chilling. The twigs were kept moist during treatment by enclosing them in plastic bags with moist tissue paper.

Modifications of the initial arrangement consisted of the following: In-between the harvesting of the fruits in June and the twigs in September, the tree of LaGem was uprooted. To replace it, a seedling tree No. 43/5 (Seedling), which needs less than 500 hours of chilling, was selected to provide the floral and vegetative buds for the second cultivar.

The floral and vegetative buds received two additional treatments of 50 and 60 days of chilling added onto the initial maximum of 40 days given to the seeds. This was found necessary because after 40 days of chilling the two cultivars were still in rest. This was indicated by failure of 50% of the buds to break when brought into a warm room.

Only data obtained from up to 50 days of chilling were used in the statistical analysis, as there was one treatment combination

at 60 days chilling which did not have sufficient material for extraction to warrant inclusion in the statistical analysis.

Methods

Extraction

The procedure was adapted from Hendershott and Walker (51). One gram fresh weight of material was initially planned for use in the extraction for plant growth regulators. This was adhered to with the floral and vegetative buds. With the seed, 5 g samples were used, because in cv. LaGold a single seed weighed close to a gram. From each seed, only the seed coat and the half of the cotyledon bearing the embryo axis were used. This was done in order to reduce the possibility of food reserves stored in the cotyledon affecting the extraction procedure.

Each sample of buds or seeds, after being macerated in a mortar, was extracted with 50 ml of absolute methanol for two hours at 0 C. This temperature was achieved by packing the container in ice and placing it in the refrigerator for the duration of the extraction period. At the end of the extraction period, the extract was filtered through glass wool and washed with three 10 ml aliquots of fresh methanol which were combined with the original extract. The combined methanol extract was evaporated to dryness in a water bath, under reduced pressure. The temperature of the water bath was maintained at 35 C. The extract was purified by dissolving the dry residue in a mixture of n-hexane and acetonitrile (40 ml/40 ml v/v) and discarding the n-hexane fraction which contained most of the fatty substances (71). The acetonitrile fraction was evaporated to dryness as described

above. The dry acetonitrile residue was then dissolved in 0.5 M sodium bicarbonate solution, pH 8.15, and extracted with three 30 ml aliquots of absolute ether. The ether was tested for peroxide with potassium iodide-starch test paper before use. The three ether washings were combined and dried with anhydrous sodium sulfate. This comprised the neutral/basic fraction of the extract. The bicarbonate solution was acidified to pH 2.8 with 10% hydrochloric acid, using a pH meter to determine the pH. The acidified solution was extracted with ether as before. This ether extract was designated the acidic fraction. The two ether extracts were concentrated to about 0.3 ml each and applied to Whatman No. 1 paper strips, 2 cm wide. The extracts were streaked in a thin line across the paper, using a 1 ml disposable syringe. The chromatograms were equilibrated with steam for 30 minutes and developed in n-butanol-ammonia-water solvent (10:1:1, v/v/v) in a Chromatocab, using the descending technique. The solvent was allowed to descend for 15 hours at a temperature of 25.5 C. The paper was then removed and dried in a hood at laboratory temperature of 22.5 C. The dried chromatograms were observed under short and long ultraviolet light, and the positions of the fluorescing and absorbing substances marked. Paper chromatograms not immediately used for bioassays were stored at -20 C.

Bioassay

The procedure was adapted from Hendershott and Walker (52), Mitchell and Livingston (69) and Walker, et al. (98). The wheat coleoptile straight growth method was used to bioassay for growth promoters and inhibitors present in the paper chromatograms.

The wheat seeds (Triticum aestivum L.) were obtained from the Seed Testing Laboratory at LSU. The cultivar Coker 68-19, Lot 0-105 was used for the bioassay of extracts from seeds. The cultivar Georgia 1123, Lot 1521 was used for the bioassay of extracts of floral and vegetative buds. The switch in cultivar was necessary because of the possibility of running short of the former cultivar.

The wheat seeds were soaked in distilled water for two hours, then seeded on moist tissue paper in germinating boxes. For the first 48 hours, the seeds were subjected to red light treatment from an incandescent red bulb placed 60 cm from the seeds. This was to suppress mesocotyl growth. After this, the seeds were allowed to germinate for another 24 hours in the dark at 24 C. Coleoptiles 15 to 25 mm long were selected. A 3-mm segment from the tip was removed. The next 4-mm segment was used for bioassay. The primary leaf was not removed from the coleoptile segments. Cutting of the coleoptiles was done under green light, provided by wrapping two 15 watt, daylight type fluorescent tubes with three layers each of amber, blue and green cellulose acetate paper. Cutting of the segments was done with a modified Wightman cutter (69). After cutting, the segments were soaked in distilled water for a maximum of three hours, to remove endogenous growth regulators.

Each paper chromatogram was divided into 10 equal parts, excluding the origin. The parts were labelled as chromatogram segments 1 to 10 from the origin. The individual segments were cut out and placed in individual 15 X 50 mm glass vials containing 1 ml of a phosphate-citrate buffer with two percent sucrose added. The buffer solution was made up of 1.798 g /liter K_2HPO_4 and 1.019 g /liter

citric acid monohydrate. The pH of the solution was 5.15. The control consisted of a vial containing a similar-sized piece of the paper chromatogram taken from above the origin, soaking in the same buffer-sucrose solution.

For the bioassay, three coleoptile segments were selected at random and placed in each vial. The vials were then covered with loose fitting caps and the coleoptiles were allowed to incubate for 20 hours in the dark at 22.5 C, after which they were removed and placed on a glass slide in a photographic enlarger and the projected shadow measured under 2 X magnification. A flexible ruler was used to make measurements in order to measure those coleoptiles which developed curvature during the incubation period. The measurements were made in mm, measured to the nearest 0.5 mm.

The average length of the three coleoptiles in each vial was then expressed as a percentage of the average length of the three coleoptiles in the control, using the formula:

$$\frac{\text{average length of treatment segment}}{\text{average length of control}} \times 100$$

Values greater than 100 were assumed to indicate the presence of a promoter and the deviations from 100 were given a positive value. Values less than 100 were assumed to indicate the presence of an inhibitor and the deviations from 100 were given a negative value. These positive and negative deviation values were used in the statistical analyses.

Statistical Analyses

Due to the replacement of cv. LaGem by Seedling to provide the floral and vegetative buds for one of the cultivars and the inclusion of an additional treatment of 50 days chilling for the floral and vegetative buds, it was not possible to analyze the experiment as a whole. Instead, the statistical analysis was carried as follows:

The data derived from the bioassays of the floral and vegetative buds of the two cultivars (LaGold, Seedling) were analyzed as a randomized block design with a split plot arrangement where cultivars served as blocks; the two bud types (floral, vegetative), and the six periods of chilling at 7.2 C (0, 10, 20, 30, 40, 50 days) served as main plot factors; the 10 chromatogram segments of each chromatogram (Rf values 0.1 to 1.0), replicated three times, served as sub-plot factors. The acidic and neutral/basic fractions were treated as two separate variables.

The same data derived from the bioassays of floral buds of cv. LaGold, up to 40 days chilling, and the data derived from the bioassays of the seed of the same cultivar were analyzed as a completely randomized design with a split plot arrangement. The two organ types (floral bud, seed) and the five periods of chilling (0, 10, 20, 30, 40 days) served as main plot factors; the 10 chromatogram segments of each chromatogram, replicated three times, served as sub-plot factors. The acidic and neutral/basic fractions served as two separate variables.

Histograms

The histograms were drawn with the 10 Rf values along the x axis against coleoptile extensions, expressed as % of control, along

the y axis. Each % of control value was the average of the three replications of each treatment combination.

Termination of the Rest Period

To determine the end of the rest period, five twigs were removed from each treatment combination and placed in the laboratory with the basal ends of the twigs in water, and subsequent bud break observed. The rest period was considered broken when 50% of the buds had emerged after 21 days.

II. Seed Germination and Seedling Characteristics

After each treatment period, a batch of seeds of each variety was germinated to determine rate of germination as well as growth characteristics of the seedlings. Each batch of seeds was treated as follows:

1. Ten seeds had their seed coats removed before being sown on moist filter paper in a petri dish.
2. Ten seeds were sown with seed coats intact.
3. Ten seeds were sown with seed coats intact, but after the seeds had been leached with running water for 30 hours.

III. Application of Extracts to Buds

This test was performed to find out whether the various zones of promotion and inhibition found on the chromatograms would influence the length of the rest period. The paper chromatograms of the acidic and neutral/basic fractions were each divided into 10 segments, plus a control taken from above the origin. Each paper segment was placed in a glass vial containing 1 ml of a buffered sucrose solution, as used

in the bioassay. A fully chilled two-noded peach twig, bearing both floral and vegetative buds was then placed in each vial. The number of days to bud break was recorded.

IV. Extraction and Bioassay of Pecan Bud Scales

Extractions were made of the bud scales of pecan, Carya illinoensis (Wang.) K. Koch., before and after 60 days of chilling at 7.2 C, to determine whether it has a similar mechanism for the regulation of rest as in the peach. One-half gram fresh weight of scales from buds of cv. Desirable was used in each replication and subjected to the same extraction and bioassay methods as for the peach.

RESULTS AND DISCUSSION

I. Promoters and Inhibitors in Floral and Vegetative Buds of Peach

In the analysis of variance for floral and vegetative buds of cultivars LaGold and Seedling, in both the acidic and neutral/basic fractions, no significant differences were found between the two cultivars, the two bud types and the six periods of chilling of 0, 10, 20, 30, 40 and 50 days. There was, however, a significant difference in the bioassay means of the 10 Rf values (Appendixes 9 and 10).

The significant difference in the Rf component could be interpreted as the presence of qualitatively different substances in the extracts, as represented by their Rf values, or quantitative differences within a qualitative entity could be involved. The bioassay means at different Rf values (Table 1), indicated that regardless of cultivars, bud types, and period of chilling, a zone of promotion was detected on the paper chromatograms by the bioassay in the acidic fraction at Rf 0.1-0.2 and possibly extending to Rf 0.3 (Fig. 1-4, Appendixes 1-4). A second zone of promotion was detected at Rf 0.7, and possibly extending to Rf 0.8. Zones of inhibition were found at Rf 0.4-0.6 and at Rf 0.8-0.9. The findings here agreed with the results of Hendershott and Walker (51), who reported the presence of a growth promoter at Rf 0.15 which they thought was indolepyruvic acid (IPyA) (87). At Rf 0.36, they found a promoter which they thought was indoleacetic acid (IAA), since pure IAA chromatographed

in the same solvent at this Rf value. This Rf value was slightly higher than the one reported by Blommaert (9, 10) at Rf 0.30 in the same solvent and slightly lower than the one reported by Nevins and Hemphill (70) at Rf 0.40 in isopropanol water. The third promoter they found averaged out at Rf 0.89. This was the zone where neutral substances like indole acetonitrile (IAN) and indole ethyl acetate (EtIA) normally occurred (Rf 0.70-1.0). Blommaert (9, 10) reported the presence of a fourth promoter at Rf 0.5, which was not apparent in this investigation nor reported by Hendershott and Walker (51). Also a promoter reported by Nevins and Hemphill (70) at Rf 0.55-0.65 was not obtained. This was the zone of peak inhibition in this investigation. The zones of inhibition at Rf 0.4-0.6 and at Rf 0.8-0.9 roughly corresponded to the zone occupied by the inhibitor naringenin in the acidic fraction of the extract of Hendershott and Walker (51).

Though Hendershott and Walker fractionated their extracts into an acidic and a neutral/basic fraction, they did not report on the latter. In the neutral/basic fraction, a promoter occurred at Rf 0.1 which occasionally extended into Rf 0.2 (Fig. 5-8, Appendixes 5-8). The nature of this substance was not determined. A distinct zone of inhibition extended from Rf 0.4-0.9 with a peak at Rf 0.7. The nature of the substances found in this zone was not determined. By deduction, the zone could be made up of phenolic substances. In the extraction procedure, the pH of the sodium bicarbonate solution used to fractionate the organic acids was 8.15 (Hendershott and Walker reported a pH of 8.75). In the presence of a weak alkali like

sodium bicarbonate, strong plant acids would be fractionated into the acidic fraction. Weaker acids like phenolic acids would be fractionated into the basic fraction. Phenolic acids have been reported to be present in peach (91). Thus in the present investigation, there were two zones of inhibition, occurring at about the same Rf values in both the acidic and neutral/basic fractions. The zone of inhibition in the acidic fraction was first designated by Bennet-Clark and Kefford (5) as inhibitor β. It was comprised of ether soluble acid inhibitors. It was found in a wide range of plants, including potato shoots and tubers, pear fruit buds, grape seeds, apple leaves and peach seeds (55, 82). It was made up of phenolic substances including o- and p-coumaric acids and salicylic acid (93). Abscisic acid was ultimately isolated from this zone and was attributed by Wareing et al. (103) to be the single inhibitor involved in the regulation of rest in buds of forest trees. Naringenin, which could be a constituent of inhibitor β, was attributed by Hendershott and Walker (51) to be the inhibitor involved in the regulation of rest in peach buds.

Table 1. Bioassay means at the 10 Rf values in the acidic and neutral/basic fractions of the floral and vegetative buds of cultivars LaGold and Seedling.[1]

Rf	No. of Observations	Acidic Fraction	Neutral/Basic Fraction
0.1	72	2.53	1.79
0.2	72	0.88	- 2.42
0.3	72	- 2.08	- 7.96
0.4	72	- 6.48	-13.89
0.5	72	-13.68	-23.43
0.6	72	-12.06	-37.79
0.7	72	- 7.56	-39.60
0.8	72	- 8.08	-36.82
0.9	72	-10.43	-28.20
1.0	72	- 8.04	- 7.98

[1]The mean at each Rf value was the average of 72 of the corresponding means derived from two cultivars, two bud types and six periods of chilling, each replicated three times. The coleoptile extensions, responding to growth promoters and inhibitors in the bioassay, expressed as deviation from the control set at 100, were used to derive these means. Deviation values greater than 100 were given positive values, and deviation values less than 100 were given negative values.

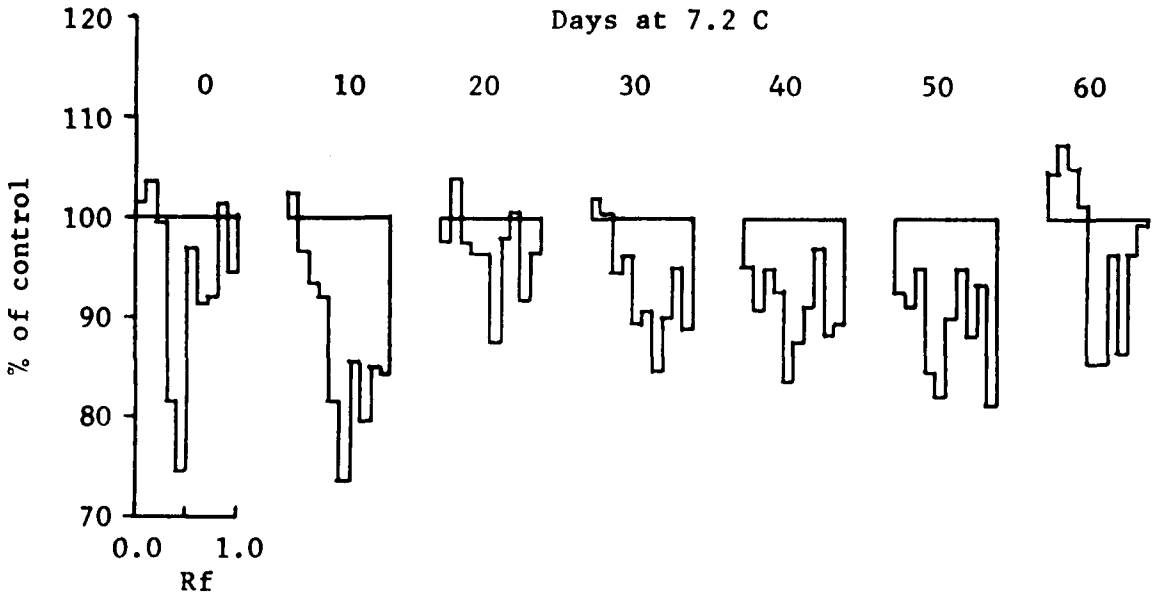

Figure 1. Responses of wheat coleoptiles to endogenous growth promoters and inhibitors, at Rf values 0.1-1.0, in the acidic fraction of ether extracts of floral buds of cv. LaGold after 0, 10, 20, 30, 40, 50 and 60 days at 7.2 C.

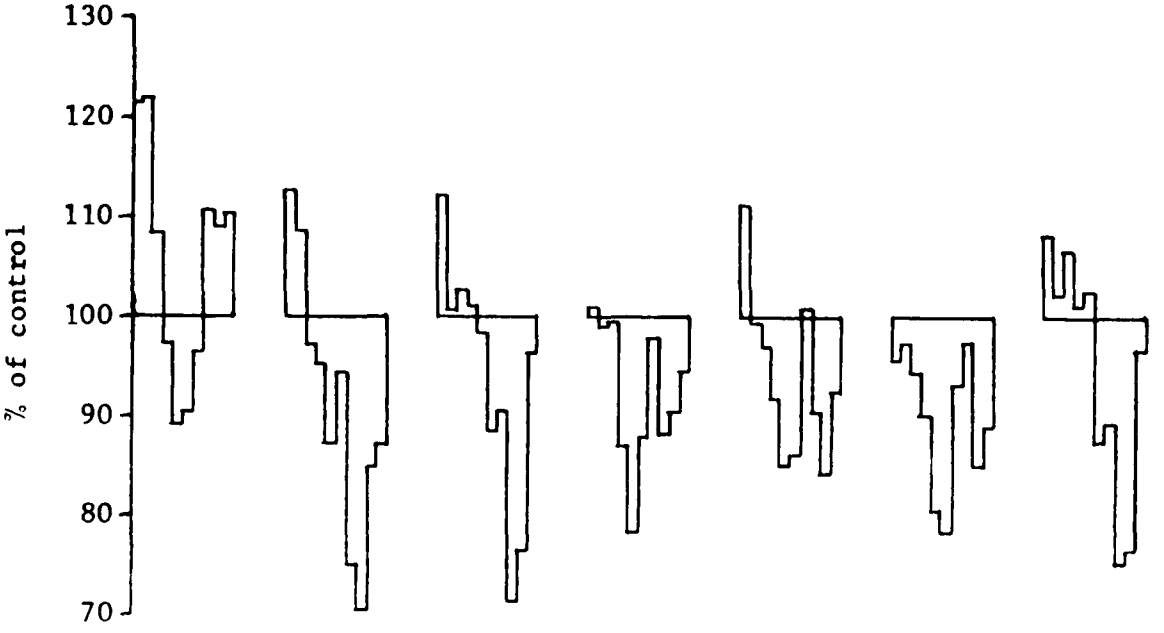

Figure 2. Responses of wheat coleoptiles to endogenous growth promoters and inhibitors, at Rf values 0.1-1.0, in the acidic fraction of ether extracts of vegetative buds of cv. LaGold after 0, 10, 20, 30, 40, 50 and 60 days at 7.2 C.

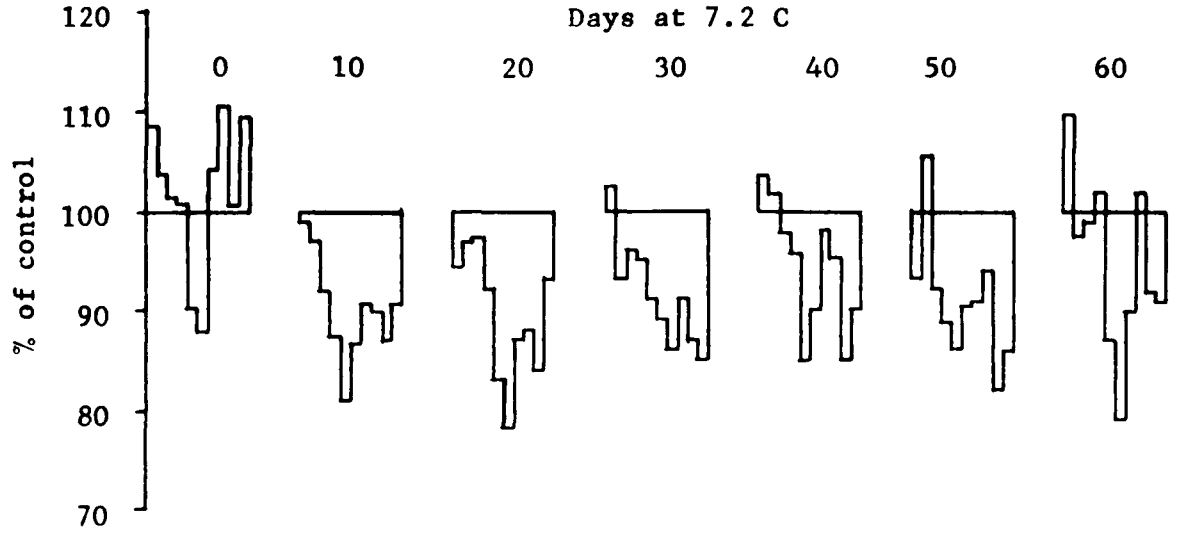

Figure 3. Responses of wheat coleoptiles to endogenous growth promoters and inhibitors, at Rf values 0.1-1.0, in the acidic fraction of ether extracts of floral buds of cv. Seedling after 0, 10, 20, 30, 40, 50, and 60 days at 7.2 C.

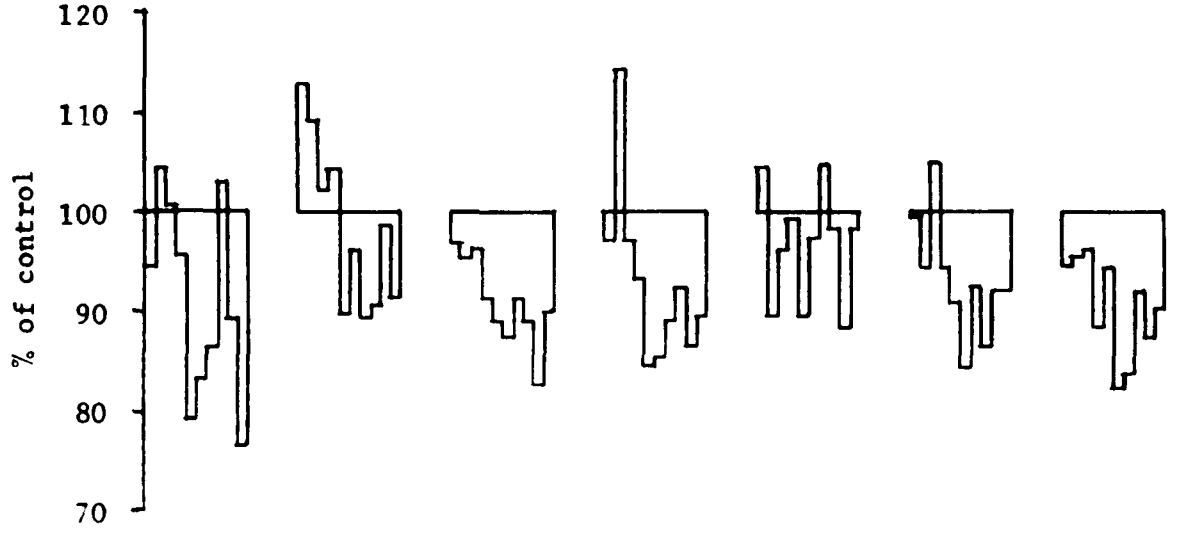

Figure 4. Responses of wheat coleoptiles to endogenous growth promoters and inhibitors, at Rf values 0.1-1.0, in the acidic fraction of ether extracts of vegetative buds of cv. Seedling after 0, 10, 20, 30, 40, 50 and 60 days at 7.2 C.

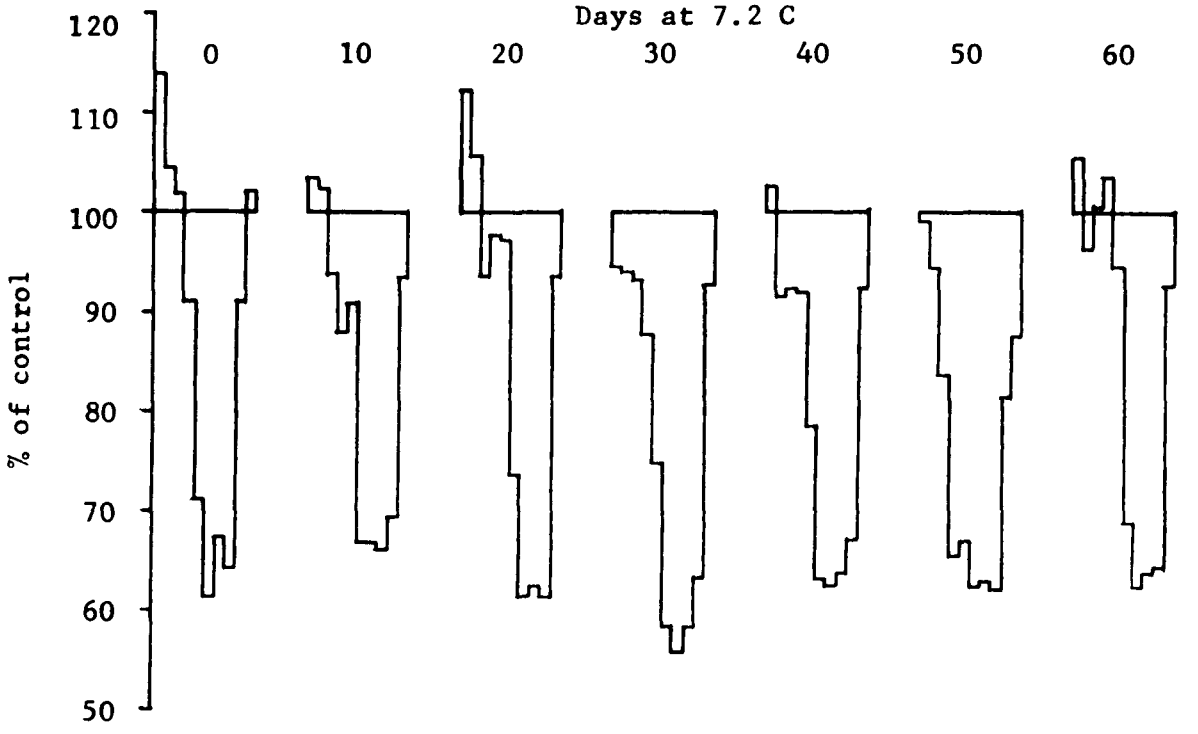

Figure 5. Responses of wheat coleoptiles to endogenous growth promoters and inhibitors, at Rf values 0.1-1.0, in the neutral/basic fraction of ether extracts of floral buds of cv. LaGold after 0, 10, 20, 30, 40, 50 and 60 days at 7.2 C.

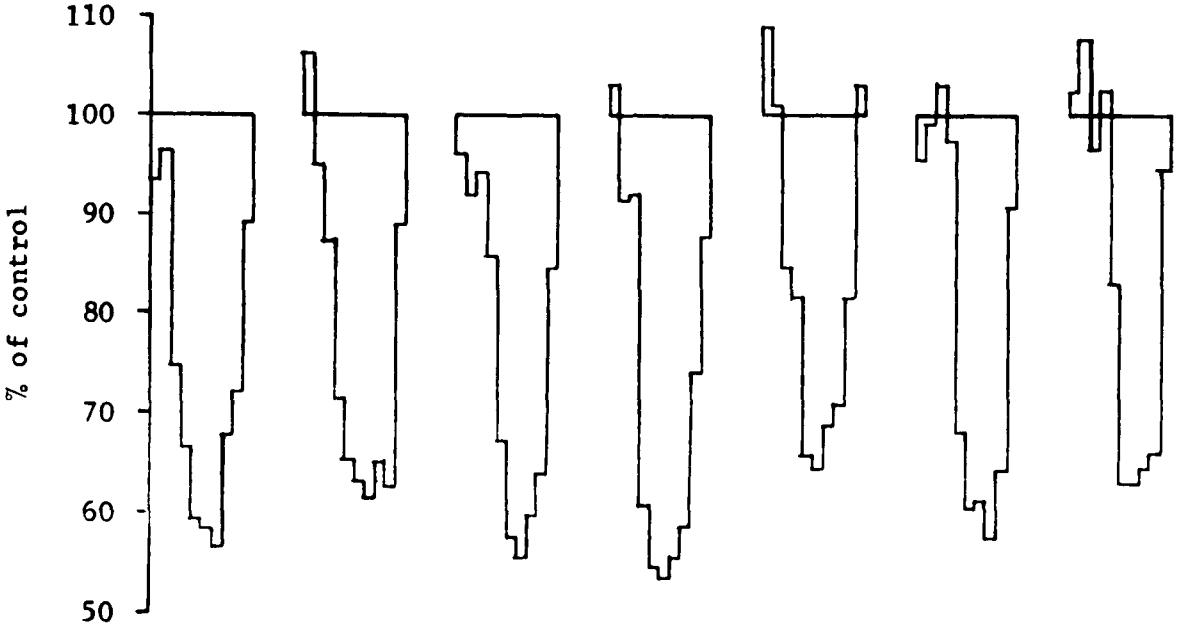

Figure 6. Responses of wheat coleoptiles to endogenous growth promoters and inhibitors, at Rf values 0.1-1.0, in the neutral/basic fraction of ether extracts of vegetative buds of cv. LaGold after 0, 10, 20, 30, 40, 50 and 60 days at 7.2 C.

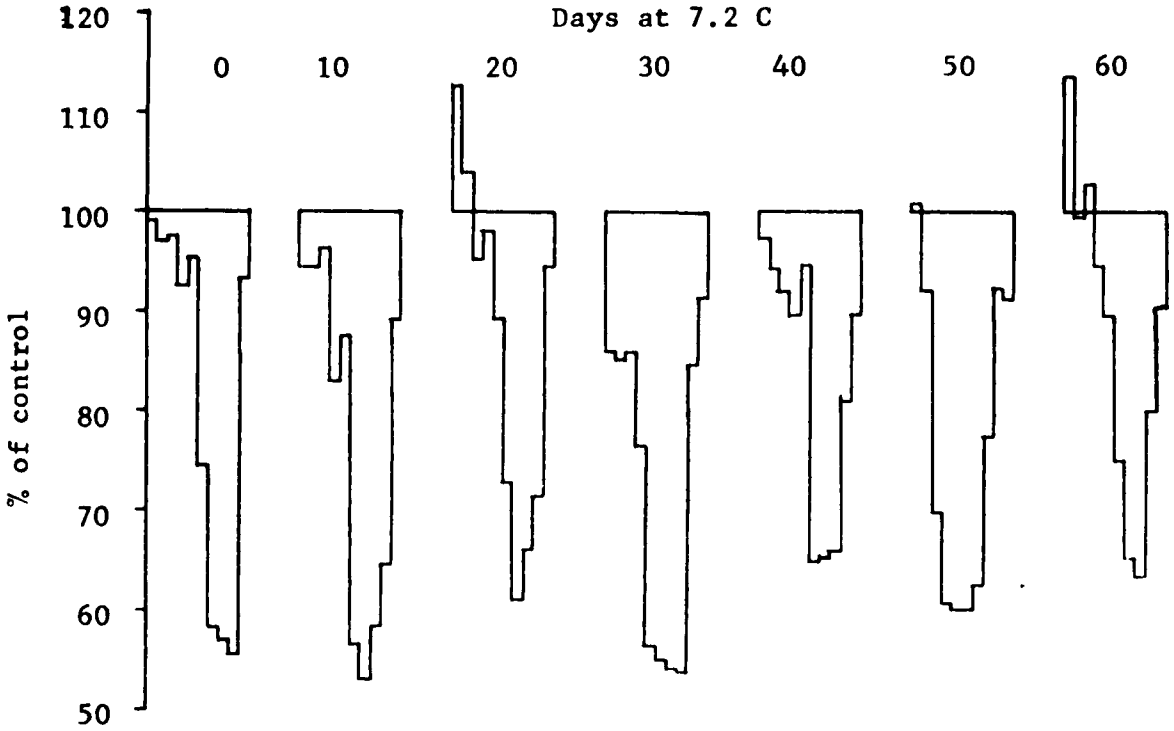

Figure 7. Responses of wheat coleoptiles to endogenous growth promoters and inhibitors, at Rf values 0.1-1.0, in the neutral/basic fraction of ether extracts of floral buds of cv. Seedling after 0, 10, 20, 30, 40, 50 and 60 days at 7.2 C.

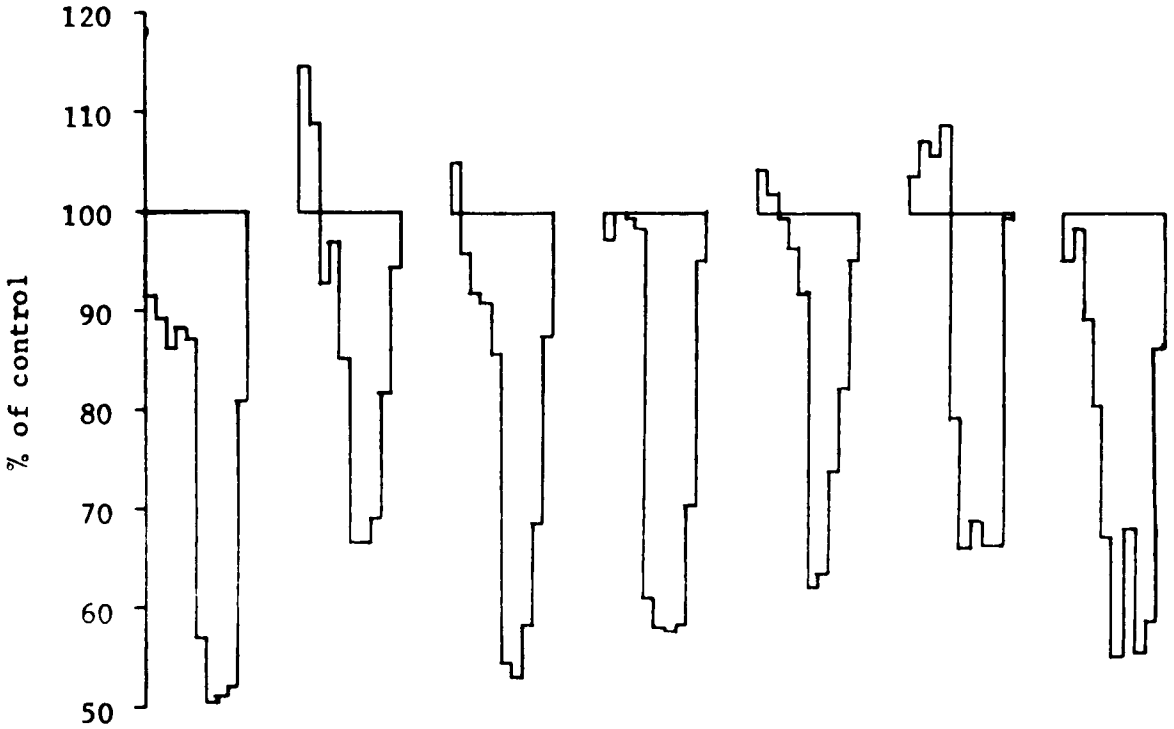

Figure 8. Responses of wheat coleoptiles to endogenous growth promoters and inhibitors, at Rf values 0.1-1.0, in the neutral/basic fraction of ether extracts of vegetative buds of cv. Seedling after 0, 10, 20, 30, 40, 50 and 60 days at 7.2 C.

II. Promoter/Inhibitor Balance Concept in the Regulation of Rest in Peach Buds.

In the analysis of variance for floral and vegetative buds of cultivars LaGold and Seedling, there were significant differences in the number of days chilling at 7.2 C X Rf interaction in both the acidic and neutral/basic fractions (Appendixes 9 and 10). The number of days chilling at 7.2 C X Rf interaction means for these fractions are shown in Tables 2 and 3. When these means were drawn with each Rf value over number of days chilling at 7.2 C (Fig. 9 and 10), there were no apparent trends which indicated an increase in the levels of promoters and a corresponding decrease in the levels of inhibitors with increasing periods of chilling in neither the acidic nor neutral/basic fractions. In fact, in the acidic fraction, at Rf 0.1 and 0.2, which indicated the presence of promoters, the levels of promoters decreased with increasing number of days of chilling.

The levels of inhibitors in both the acidic and neutral/basic fractions remained high, even when rest was broken in the cultivar Seedling after 50 days at 7.2 C, as indicated by 50% of the buds breaking in 21 days when twigs were brought into a warm room (105). This did not agree with the results of Hendershott and Walker (51) and Blommaert (9, 10) who reported that there was a rise in promoter levels and a drop in the inhibitor level two weeks before bloom. It has to be noted that the present investigation was carried out using excised twigs with continuous chilling whereas Hendershott and Walker (51) used intact twigs subjected to natural winter conditions, though the method of evaluating the end of rest was the same.

Table 2. Days of chilling x Rf interaction means in the acidic fraction of the floral and vegetative buds of LaGold and Seedling.[1]

	Number of Days Chilling at 7.2 C					
Rf	0	10	20	30	40	50
0.1	8.18	6.75	0.45	0.68	3.79	- 4.69
0.2	8.51	2.92	- 0.83	1.81	- 4.49	- 2.65
0.3	2.45	- 3.67	- 1.39	- 3.15	- 3.48	- 3.22
0.4	- 5.93	- 5.08	- 4.33	- 7.94	- 4.97	-10.64
0.5	-16.61	-15.12	- 7.10	-13.94	-14.23	-15.05
0.6	-10.29	-12.26	-14.52	-11.58	- 9.46	-14.26
0.7	- 5.32	-14.69	- 8.11	-10.37	- 1.17	- 5.70
0.8	3.99	-17.22	-12.94	- 9.17	- 4.50	- 8.64
0.9	0.01	-10.93	-16.46	-10.13	-13.40	-11.72
1.0	- 2.14	-11.48	- 5.88	-10.47	- 5.56	-12.67

Table 3. Days of chilling x Rf interaction means in the neutral/basic fraction of the floral and vegetative buds of LaGold and Seedling.[1]

	Number of Days Chilling at 7.2 C					
Rf	0	10	20	30	40	50
0.1	- 0.56	4.52	6.55	- 4.72	3.22	1.71
0.2	- 2.85	0.16	- 0.79	- 7.28	- 2.79	- 0.95
0.3	- 9.71	- 7.31	- 6.17	- 7.45	- 7.76	- 9.35
0.4	-15.42	-14.94	- 6.79	-19.30	- 9.97	-16.90
0.5	-21.64	-17.94	-14.83	-38.09	-17.14	-31.23
0.6	-36.98	-36.80	-35.32	-43.72	-36.26	-37.64
0.7	-41.86	-37.90	-42.40	-43.94	-34.93	-35.99
0.8	-39.23	-35.24	-38.39	-42.53	-31.56	-33.95
0.9	-32.26	-30.56	-33.76	-26.89	-22.04	-23.68
1.0	- 8.52	- 8.40	-10.13	- 8.00	- 5.10	- 7.75

[1]The interaction means at each Rf value was the average of 12 of the corresponding means derived from two cultivars and two bud types, each replicated three times. The coleoptile extensions, responding to growth promoters and inhibitors in the bioassay, expressed as deviation from the control set at 100 were used to derive these means. Deviation values greater than 100 were given positive values, and deviation values less than 100 were given negative values.

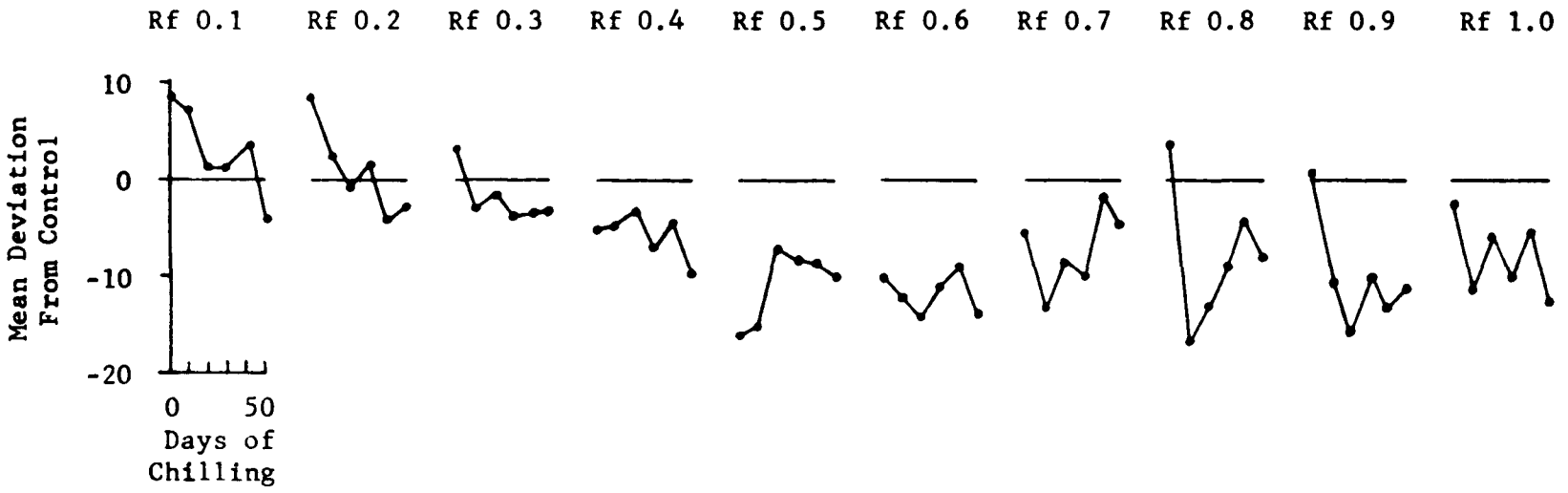

Figure 9. Responses of wheat coleoptiles to endogenous growth promoters and inhibitors in the acidic fraction of the floral and vegetative buds of cv. LaGold and Seedling at each Rf value for chilling periods of 0, 10, 20, 30, 40, and 50 days at 7.2 C.

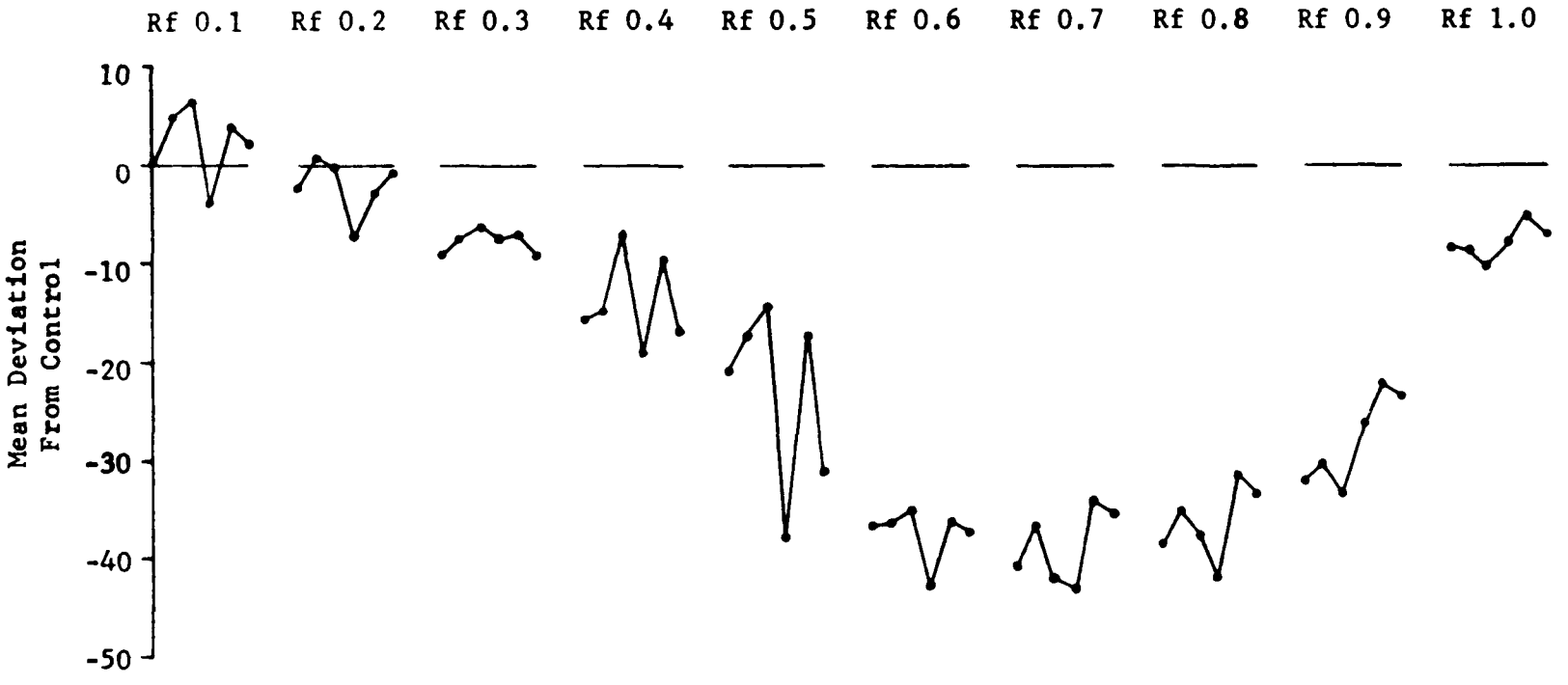

Figure 10. Responses of wheat coleoptiles to endogenous growth promoters and inhibitors in the neutral/basic fraction of the floral and vegetative buds of cv. LaGold and Seedling at each Rf value for chilling periods of 0, 10, 20, 30, 40, and 50 days at 7.2 C.

With bioassays specifically for GA, Chailakhian, et al. (16) found higher levels of GA-like activity in buds of the peach following cold treatment. El-Antably (35) working with Ribes nigrum also found a progressive increase in promotion activity in buds subjected to natural winter conditions as well as in buds which had been excised and stored in a cold room at 2 C. He too used a bioassay specific to GA.

The wheat coleoptile straight growth assay is a test mainly for auxins and inhibitors and is not too sensitive to GA. The presence of inhibitors could mask the action of the promoters, thus possibly accounting for the low levels of promoters detected.

Prior to a discussion on the high levels of inhibitors present when rest was broken, as reported here, an evaluation of the criterion for the determination of the breaking of rest may be helpful. A question could be raised as to the reliability of this method of bringing excised twigs indoors into a warm room and waiting for 50% of the buds to break as an indication of the end of the rest period. This method was first used by Chandler (17) and has since been used by others (20, 50, 51, 105, 110). Normally it took about 10-15 days for buds to break in the warm room, after the twigs had received sufficient chilling. Thus, was there a further shift in the balance of promoters and inhibitors during this period while waiting for the buds to break? Radley (77) has reported that with spinach (Spinacia oleracea), if plants which had been growing under short day conditions were exposed to even a single long day cycle, there was a marked increase in the level of GA. He suggested that the rapid increase was due to conversion of an inactive form of GA to an active form. Thomas, et al.

(88), working with birch, thought that the rapid increase was due to de novo synthesis of GA. In this investigation, when the peach twigs were brought into a warm room, under the relatively long day conditions existing in the laboratory, a growth promoter could be formed which tipped the balance in favor of growth. On the other hand, there could have been a breakdown of the inhibitors during this period. The shock of excision could be a factor too.

A second possibility could be that not all the inhibitors detected by the bioassay would be involved in the regulation of rest. So far, two groups of inhibitors have been reported to be present in peach. One was phenolic in nature, including naringenin, and the other was ABA - a terpenoid substance. None of these substances has been conclusively shown to be involved in the regulation of rest. A test carried out to determine which of the inhibitors detected in the current investigation was involved in rest, by re-application of extracts of the paper chromatogram segments to peach twigs bearing fully chilled buds, was inconclusive, due to high mortality rates in the test materials during the test.

A third possible explanation to account for the high levels of inhibitors could be that, though the inhibitors were present, they have been prevented from exerting their influence by the mechanism proposed here.

The inhibitors may have been mainly in the scales. Dennis and Edgerton (30) reported that 80% of the inhibitors in the peach bud were found in the scales. The inhibitor currently thought to be involved in the regulation of rest is abscisic acid. Besides being an inhibitor of growth, ABA is also responsible for abscission (2).

It is proposed that as the bud primordium was developing in the bud, ABA, responding to a "message", caused the formation of abscission layers in the senescing outer scales, which thus reduced the influence of the inhibitors on the bud primordium, to the extent that growth could occur, if the environmental conditions were favorable.

Three observations lent support to this proposal. It was found in this investigation that removal of all the scales from the bud primordia on intact twigs resulted in bud break four weeks later (Plate 1). The control buds with scales intact failed to flower or leaf out.

Using excised twigs, it was observed that as the leaf bud emerged from rest, the scales were pushed up on the tips of the elongating leaves (Plate 2). This would imply that an abscission layer must have been formed earlier, which could have blocked the action of the inhibitor on the bud primordium.

With the floral buds, it was observed that as the buds were emerging from rest, the scales were pushed out and could be easily detached along a line of abscission (Plate 3). Again, this would imply that an abscission layer must have been formed earlier, and this could have blocked the action of the inhibitor on the floral primordium.

Corgan (21) in 1964, reporting before the establishment of ABA as a growth inhibitor and abscission accelerant, suggested that rest could be controlled by diffusion of naringenin from bud scales into flower primordium. If so, he postulated that any morphological or physiological change which interfered with this diffusion could terminate rest. Thus this proposal here of the formation of an

abscission layer by ABA could be the interference to the diffusion of the inhibitor to the bud primordium.

Another mechanism which could cause bud break in the presence of high inhibitor levels was reported by Tinklin and Schwabe (90). Working with blackcurrants, they found that the bud scales were the main cause of inhibition. Bud break resulting from brief exposure to very low temperatures (-15 C) was attributed by them to be almost certainly the result of killing the scales. This would imply that the transfer of the inhibitor to the bud primordium depended on the bud scales being alive.

Applied to the peach, one problem of the freezing proposal would be that under natural conditions, the vegetative buds generally break out later than the floral buds. But vegetative buds generally have only six to seven scales as compared to 13 to 15 scales per floral bud. Thus one would expect the vegetative bud with a lesser number of scales to leaf out faster than floral buds. This was not so. On the other hand, the vegetative buds are generally sandwiched between the floral buds and this could be sufficient protection against freezes which killed the more exposed scales of the floral buds.

Except for Dennis and Edgerton (30), who bioassayed the bud and scales separately, all others have used whole buds, and this point of an abscission barrier would have been missed.

Verification of this proposal, correlating formation of abscission layer and inhibitor levels may throw more light on the subject of regulation of rest in buds based on the concept of a balance of growth promoters and inhibitors.

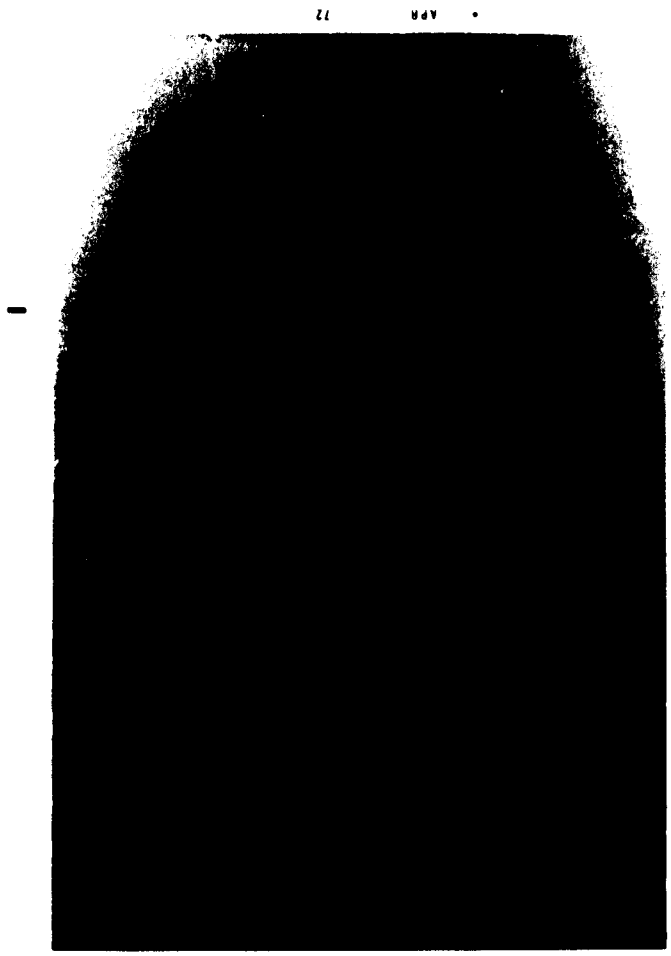

Plate 1. Bud break of peach after removal of bud scales.

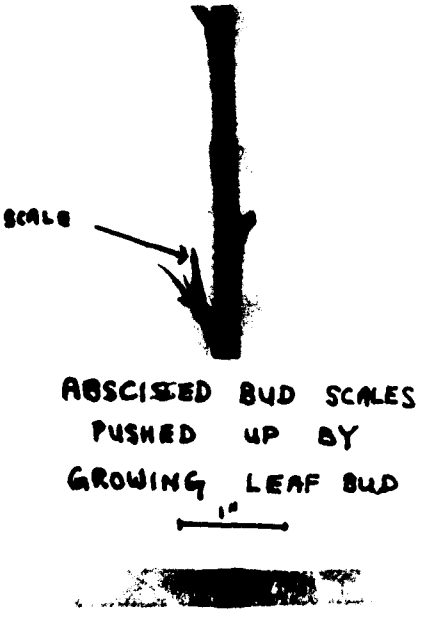

Plate 2. Abscised bud scales of peach being pushed up by growing leaf bud.

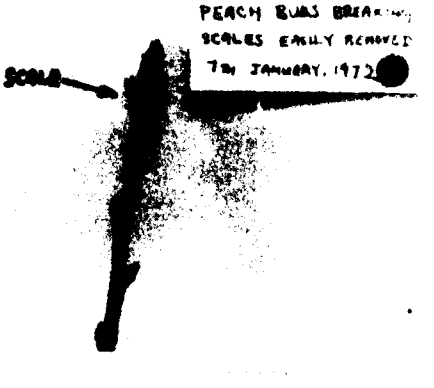

Plate 3. Peach floral bud breaking. Bud scales were pushed out and could be easily detached along a line of abscission.

III. Promoters, Inhibitors, and the Balance Concept in the Regulation of Rest in Peach Seed.

Freshly harvested peach seeds of the cultivars LaGold and LaGem had high levels of an inhibitor in the acidic fraction of the extract (Fig. 11 and 12, Appendixes 11 and 12). It ranged from Rf 0.2-1.0. There was a zone of promotion at Rf 0.1 in both cultivars and possibly another one at Rf 0.8, but whose effect was probably masked by the inhibitor in the cultivar LaGold. The inhibitor decreased upon chilling up to 30 days, after which the inhibitor increased to attain the original levels after 40 days of chilling. The nature of the substance was not determined.

In the neutral/basic fraction of the two cultivars, there did not appear to be definite zones of promotion or inhibition (Fig. 13 and 14, Appendixes 13 and 14). Peak activity of the zone of promotion varied from Rf 0.5 to Rf 0.8. The nature of the substance was not determined. There could probably be zones of inhibition at Rf 0.3-0.5 and another at Rf 0.9-1.0. Their presence, however, was inconsistent and did not appear to follow any trends.

In unchilled seeds, it appeared that the inhibitor was in the seed coat (Table 4) because with seed coat intact, unchilled seeds took 22 days to germinate. Leaching up to 30 hours did not appear to improve germination ability of the seed. However, removal of seed coat hastened germination by at least 17 days.

In most cases, chilling up to 30 days hastened germination. With the increase of the inhibitor to attain the original levels, after 40 days of chilling, germination was delayed by 7 days. It appeared that the cotyledons were the source of the inhibitory material,

for in the treatment where the seed coat was removed, germination was delayed, as were the other two treatments where seed coats were intact. The reason for the second peak of inhibitor was not known.

Seedlings obtained after all periods of chilling were dwarfed with malformed leaves.

Table 4. Effects of cultivars, seed coat removal, leaching and chilling on germination of peach seeds.[1]

Treatment	Cultivar	Number of Days at 7.2 C				
		0	10	20	30	40
		Number of Days to Germination				
1. Seed coats removed	LaGold	4	3	3	3	10
	LaGem	5	3	3	3	10
2. Seed coats intact	LaGold	22	23	7	10	10
	LaGem	22	23	7	3	10
3. Seed coats intact, 30 hrs. leaching	LaGold	24	16	6	2	9
	LaGem	25	16	6	2	9

[1]The criteria for determining germination were: In Treatment 1, when the radical had attained a length of 2 mm; and in Treatments 2 and 3, when the seeds had split coats. There were 10 seeds per treatment combination.

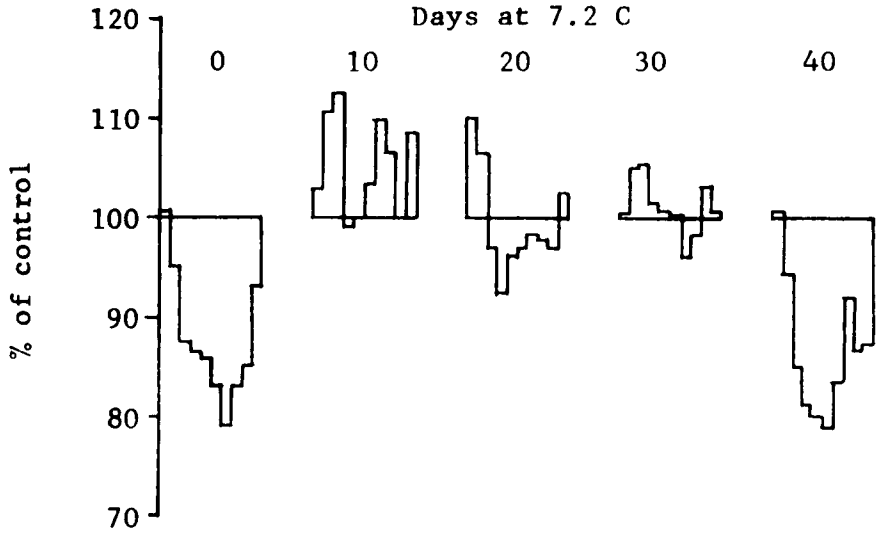

Figure 11. Responses of wheat coleoptiles to endogenous growth promoters and inhibitors in the acidic fraction of seed of cv. LaGold after 0, 10, 20, 30 and 40 days at 7.2 C.

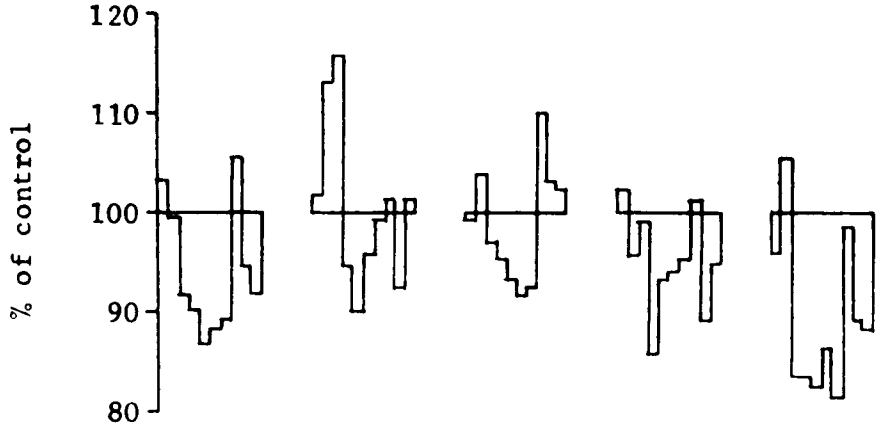

Figure 12. Responses of wheat coleoptiles to endogenous growth promoters and inhibitors in the acidic fraction of seed of cv. LaGem after 0, 10, 20, 30 and 40 days at 7.2 C.

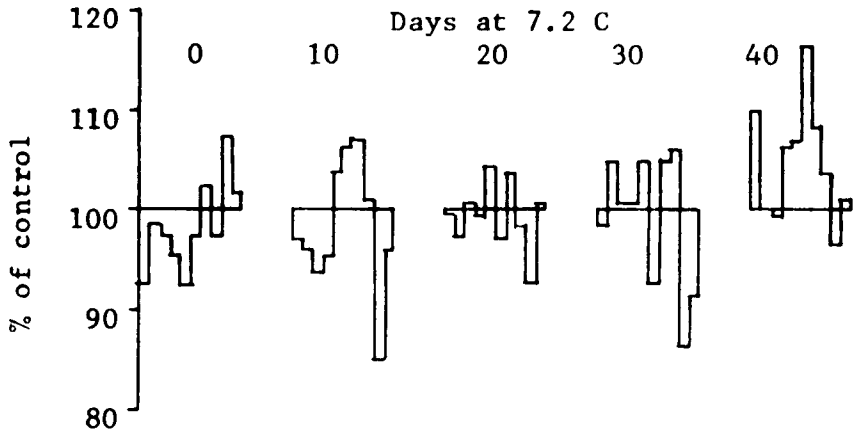

Figure 13. Responses of wheat coleoptiles to endogenous growth promoters and inhibitors in the neutral/basic fraction of seed of cv. LaGold after 0, 10, 20, 30 and 40 days at 7.2 C.

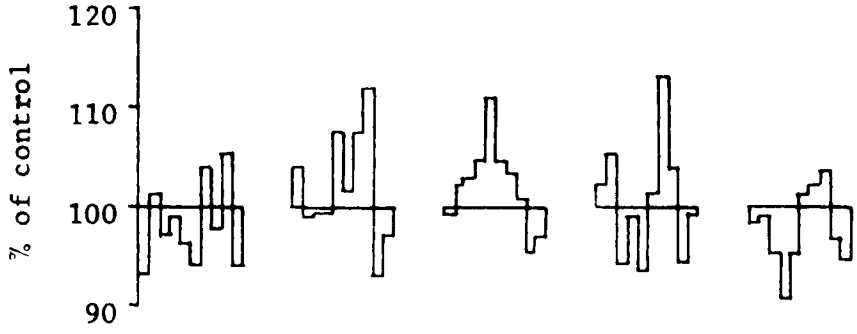

Figure 14. Responses of wheat coleoptiles to endogenous growth promoters and inhibitors in the neutral/basic fraction of seed of cv. LaGem after 0, 10, 20, 30 and 40 days at 7.2 C.

Liao (62) thought that the inhibitor was naringenin. Ryugo (82), Lipe and Crane (63) attributed it to ABA with the seed coat having the highest concentration. The latter authors correlated end of rest with the disappearance of the inhibitor. With hazel, less than 1% of total inhibition was attributed to ABA (13). In ash, during chilling ABA decreased by 37% in the pericarp and 68% in the seed.

Recent evidence favors a balance of GA/ABA in the regulation of dormancy in Fraxinus excelsior seed (82, 101). With the peach, evidence was conflicting and inconclusive. With a wheat coleoptile assay, Liao (62) reported a gradual decline in inhibitor level upon chilling and promoter levels remained relatively constant. Similar results were reported by Biggs (7). In a more detailed work, Wong and Edgerton (109) found no correlation between chilling and inhibitor (ABA) in the seed coat, cotyledon and embryo axis. Again promoter levels remained relatively constant. Mathur et al. (65) found that percentage germination increased as GA_3 and GA_7 increased during stratification. This GA synthesis occurred at 0 C and not at ambient temperatures. Bradbeer (13), working with hazel concluded that chilling (5 C) activated GA synthesis, and subsequent synthesis was at the germination temperature of 20 C.

Exogenous GA could break the rest in peach seeds (19, 31), but not of floral buds (44), lending support to the interpretation that a different mechanism may be involved in the regulation of rest in these two organs.

Though recent evidence favors a GA/ABA interaction, in rare cases, a combination of GA and kinetin was required to overcome the effect of ABA (86, 107). The little mention of cytokinins could

be due to the technical difficulty of purifying and assaying this type of hormone. Wareing and Saunders (101) suggested that the approach to this problem of regulation of rest using bioassay techniques had probably been taken as far as was profitable. As a next step, they called for positive identification of compounds involved and precise quantities determined. Upon which we might find that it was not all along a one substance one action theory upon which most of the efforts had been directed (84). The model of seed dormancy of Amen (4) might be headed in the right direction with its overall approach (Fig. 15).

Rest Mechanism in Floral Bud, Vegetative Bud and Seed of Peach

Comparing the histogram patterns of both the acidic and neutral/basic fractions of the floral and vegetative buds of the two cultivars LaGold and Seedling (Fig. 1-8), it appeared that the patterns were generally similar. In the acidic fraction, zones of promotion appeared at Rf 0.1 to 0.2 and 0.7 to 0.8. Zones of inhibition were found at Rf 0.4-0.6 and at Rf 0.8-0.9. In the neutral/basic fraction, a zone of promotion occurred at Rf 0.1 in many treatments. This zone of promotion extended to Rf 0.2 and 0.3 in some treatments. In those treatments which did not show a zone of promotion at Rf 0.1, its effect could have been masked by a conspicuous zone of inhibition which was most pronounced at Rf 0.4 to 0.9

In the histogram patterns of the acidic and neutral/basic fractions derived from the seeds of cultivars LaGold and LaGem (Fig. 11-14), there was a zone of promotion at Rf 0.1 in the acidic

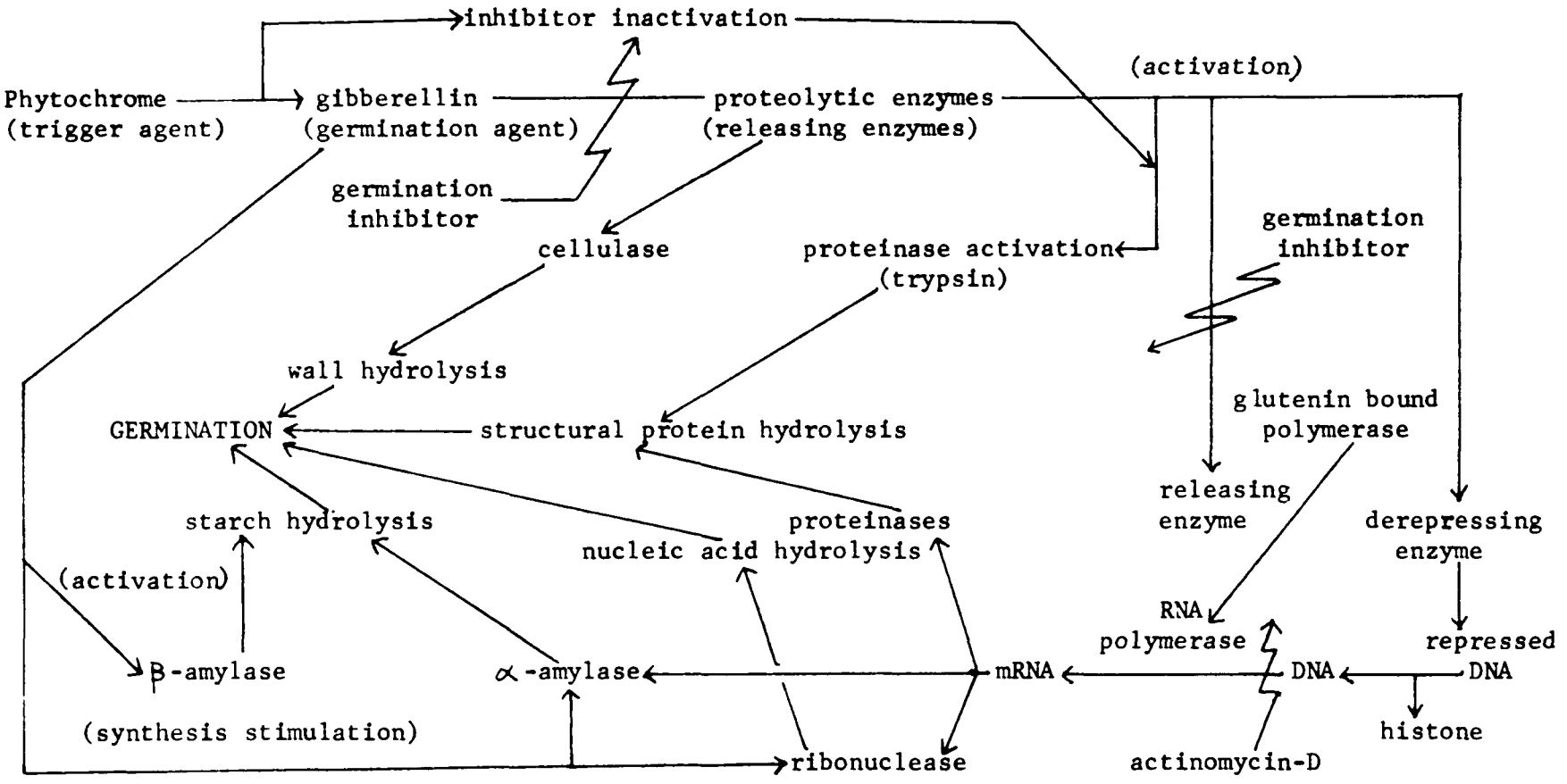

Figure 15. Possible biochemical pathways in the termination of seed dormancy. (4)

fraction in both cultivars, and possibly another one at Rf 0.8, but its effect was probably masked by the inhibitor, especially at 40 days chilling. In the neutral/basic fraction, promoters appeared to dominate, with peaks at different Rf values. Distinct zones of inhibition were not clearly discernable.

The most distinct difference between the histogram patterns of the seed and those of the floral and vegetative buds was the complete absence of a conspicuous zone of inhibition at Rf 0.4 to 0.9 in the neutral/basic fraction of the seed. It thus appeared that the rest period in both the floral and vegetative buds could be regulated by a similar mechanism involving identical growth promoters and inhibitors, but a different mechanism or at least different growth promoters and inhibitors could be involved in the regulation of rest in the seed.

One gram fresh weight of floral and vegetative buds and 5 g fresh weight of seeds were used in the extractions. The effects of the difference in fresh weight of materials used on the bioassay were not determined.

In the analysis of variance for the floral and vegetative buds of the cultivars LaGold and Seedling, non-significant differences were found between the two cultivars, the two bud types and the different periods of chilling in both the acidic and neutral/basic fractions (Appendixes 9 and 10). This lent support to the proposal that probably the same proposed mechanism could be involved in the regulation of rest in both the floral and vegetative buds of peach.

In the analysis of variance for the floral bud and seed of cv. LaGold, there was a significant difference between the two organs in both the acidic and neutral/basic fractions (Appendixes 15 and 16). This lent support to the interpretation that a different mechanism could be involved in the regulation of rest in the seed.

Table 5 shows the differences in the means of the seed in the acidic and neutral/basic fractions, compared with the means of the floral and vegetative buds in the cultivars LaGold and Seedling.

Table 5. Effects of sources of acidic and neutral/basic fractions on growth of wheat coleoptiles.

		Deviation of Control	
Organ Type	Cultivar	Acidic Fraction	Neutral/Basic Fraction
Floral Bud	LaGold	-7.97	-18.17
	Seedling	-6.62	-19.93
Vegetative Bud	LaGold	-5.40	-22.93
	Seedling	-6.02	-17.44
Seed	LaGold	-3.49	- 0.13

[1]Each mean of the floral and vegetative buds was the average of 180 values derived from six periods of chilling, 10 Rf values, each replicated three times. The coleoptile extensions, responding to growth promoters and inhibitors in the bioassay, expressed as deviation from the control set at 100 were used to derive these means. Deviation values greater than 100 were given positive values, and deviation values less than 100 were given negative values. The mean of the seed was the average of 150 values derived from five periods of chilling, 10 Rf values, each replicated three times.

IV. Regulation of Rest in Pecan

The pecan might have a similar mechanism for the regulation of rest as proposed for the peach. In the pecan, the line of abscission in the bud scale was more pronounced (Plate 4). It was observed that prior to the emergence of the bud, the bud scale abscised along the line of abscission, followed by a splitting of the cap-like scale before the bud emerged (Plate 5).

The bioassay of the acidic fraction of the bud scales indicated a zone of inhibition at Rf 0.5-0.7 corresponding roughly to similar zones in peach. In the neutral/basic fraction there was a zone of inhibition at Rf 0.7-1.0. This was at a higher Rf value compared to the peach. The nature of the substances was not determined (Fig. 16 and 17, Appendixes 17 and 18).

Plate 4. Pecan bud showing pronounced line of abscission on the bud scale.

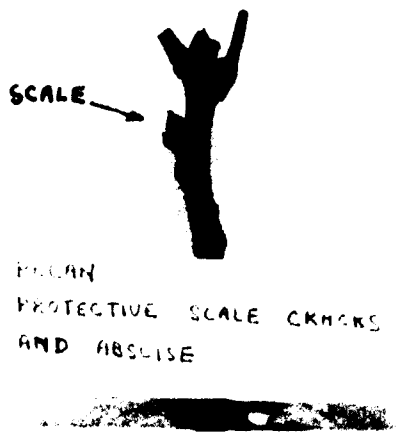

Plate 5. Pecan bud breaking following abscission along line of abscission and cracking of cap-like scale.

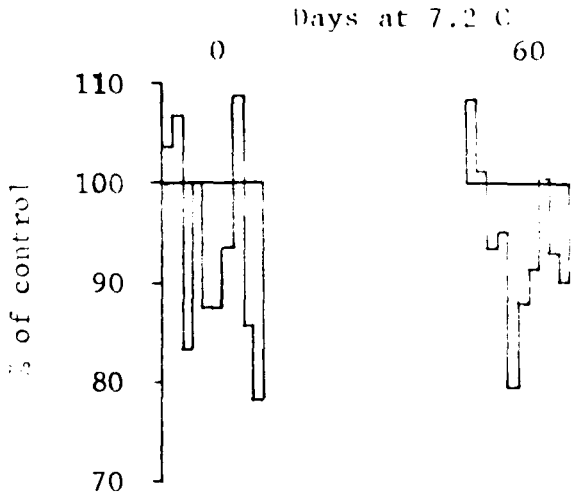

Figure 16. Responses of wheat coleoptiles to endogenous growth promoters and inhibitors, at Rf values 0.1-1.0, in the acidic fraction of ether extracts of bud scales of pecan, cv. Desirable, after 0 and 60 days at 7.2 C.

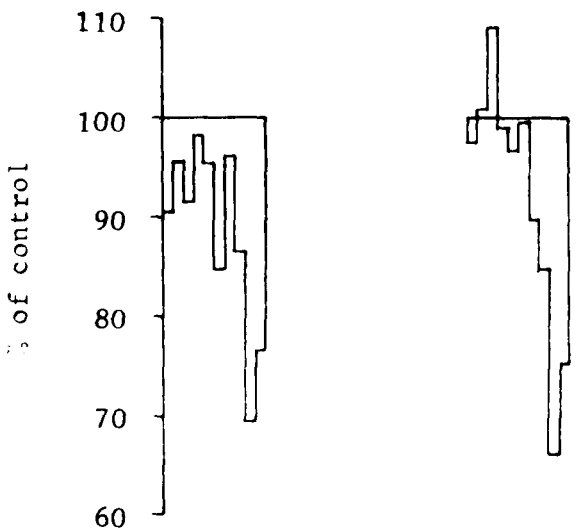

Figure 17. Responses of wheat coleoptiles to endogenous growth promoters and inhibitors, at Rf values 0.1-1.0, in the neutral/basic fraction of ether extracts of bud scales of pecan, cv. Desirable, after 0 and 60 days at 7.2 C.

SUMMARY

Chromatographs of the acidic fraction of floral and vegetative buds of peach had two zones of promotion. The promoters found at Rf 0.1-0.2 could probably be indolepyruvic acid and indoleacetic acid. The second zone of promotion at Rf 0.7 could be due to indole acetonitrile and indole ethyl acetate. Zones of inhibition were found at Rf 0.4-0.6 and at Rf 0.8-0.9, the constituents of which could probably be naringenin or abscisic acid.

Chromatographs of the neutral/basic fraction had a zone of promotion at Rf 0.1, which was of an unknown nature. A zone of inhibition at Rf 0.4-0.9 could probably be composed of phenolic acids.

Chromatographs of the acidic fraction of unchilled seeds had a zone of promotion at Rf 0.1, followed by a zone of inhibition from Rf 0.2-1.0. The inhibitor decreased upon chilling up to 30 days and then increased to the original levels after 40 days of chilling. The nature of the substances was not determined.

There did not appear to be definite zones of promotion in chromatographs of the neutral/basic fraction of extracts from seed. The presence of zones of inhibition was inconsistent and did not follow any trends.

Seedlings grown after all periods of chilling were dwarfed with malformed leaves.

Data obtained in this study did not suggest that a promoter/inhibitor balance was involved in the regulation of rest in peach buds.

The results indicated that the rest period in both the floral and vegetative buds could probably be regulated by the same mechanism involving identical substances.

A proposal was made which could account for high levels of inhibitors in the acidic and neutral/basic fractions of both bud types when rest was broken. The proposal was that abscisic acid, probably one of the many inhibitors found mainly in the scales, responding to a "message", caused the formation of abscission layers in the scales, which thus reduced the influence of the inhibitors on the bud primordium, to the extent that growth could occur if the environmental conditions were favorable. This proposal was based on observations that emerging buds have scales which could be easily detached along lines of abscission, implying that abscission layers were laid down previously.

The seed of peach probably have a different mechanism for the regulation of rest from that of the floral buds. The seed response to chilling differed from that of the floral buds, and the growth promoters and inhibitors did not appear to be similar as they occurred at different Rf values in the chromatographs.

Results obtained from pecan buds indicated that they could have a mechanism for regulation of rest similar to that of peach buds. The emergence of pecan buds followed abscission of bud scales along a distinct line of abscission and splitting of the cap-like scales. The chromatographs indicated presence of zones of inhibition in both the acidic and neutral/basic fractions which corresponded to similar zones in peach.

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Appendix 1.

Days at 7.2 C	Chromatogram Segments									
	1	2	3	4	5	6	7	8	9	10
0	101.8	103.4	99.3	81.5	74.3	96.9	91.2	92.0	101.5	94.7
10	102.4	96.6	93.3	92.2	81.6	73.8	85.5	79.3	85.0	84.5
20	97.8	104.0	97.6	96.2	96.4	87.5	98.0	100.2	91.3	96.4
30	101.9	100.1	94.3	96.1	89.6	90.8	84.6	90.0	95.3	88.7
40	95.6	90.6	94.9	92.5	83.6	87.8	91.2	97.2	88.4	89.7
50	92.7	91.7	95.1	84.2	82.1	89.9	95.0	88.0	93.4	81.5
60	104.6	107.2	105.2	101.1	85.7	85.7	96.4	86.6	96.4	99.0

Appendix 2.

Days at 7.2 C	Chromatogram Segments									
	1	2	3	4	5	6	7	8	9	10
0	121.3	121.9	108.6	97.5	89.6	90.5	96.5	110.7	109.1	110.5
10	112.6	108.1	97.2	95.4	87.1	94.1	75.0	70.5	85.0	87.1
20	112.2	100.6	102.6	101.2	98.7	88.4	90.5	71.2	76.2	96.5
30	101.2	99.3	99.6	87.1	78.7	88.4	98.1	88.0	90.5	94.7
40	111.1	99.8	97.0	91.8	85.2	86.1	100.7	90.6	84.1	92.6
50	95.2	97.4	94.8	90.0	80.5	78.4	93.4	97.3	85.0	89.0
60	108.4	102.6	106.9	101.3	102.4	87.9	89.6	75.7	76.8	96.9

Appendixes 1 and 2. Responses of wheat coleoptiles to endogenous growth promoters and inhibitors in the acidic fraction of ether extracts from peach floral buds (Appendix 1) and vegetative buds (Appendix 2) of cv. LaGold after 0, 10, 20, 30, 40, 50, 60 days of continuous chilling at 7.2 C. The data are expressed as percentage of the control and each value is the average of three replications.

Appendix 3.

Days at 7.2 C	Chromatogram Segments									
	1	2	3	4	5	6	7	8	9	10
0	108.2	103.9	101.5	101.4	90.3	88.0	104.5	110.8	100.5	109.6
10	99.0	97.4	92.0	87.6	81.1	86.9	91.1	90.4	87.4	90.9
20	94.6	97.2	97.8	92.8	83.6	78.1	87.6	88.0	84.0	93.4
30	102.5	93.8	96.5	95.3	91.6	89.1	86.8	91.8	87.3	85.3
40	103.9	102.0	98.2	96.1	85.1	90.6	98.7	95.6	85.6	90.1
50	93.6	105.7	92.7	89.0	86.3	90.2	90.3	94.1	82.1	86.1
60	109.8	97.5	99.1	101.9	87.7	79.2	90.1	101.9	92.0	91.0

Appendix 4.

Days at 7.2 C	Chromatogram Segments									
	1	2	3	4	5	6	7	8	9	10
0	94.8	104.9	100.3	95.9	79.4	83.2	86.5	102.5	89.0	76.7
10	113.0	109.6	102.8	104.5	89.8	96.1	89.8	91.0	98.9	91.5
20	97.2	95.9	96.6	91.5	89.0	87.6	91.4	88.9	82.7	89.9
30	97.1	114.1	97.1	92.8	84.4	85.5	89.0	93.5	86.5	89.5
40	104.6	89.6	96.1	99.7	89.1	97.7	104.4	98.6	88.1	98.2
50	99.8	94.6	104.6	94.4	90.9	84.4	92.4	86.1	92.6	92.7
60	94.9	95.3	96.2	88.1	94.7	82.3	83.8	92.7	87.2	90.1

Appendixes 3 and 4. Responses of wheat coleoptiles to endogenous growth promoters and inhibitors in the acidic fraction of ether extracts from peach floral buds (Appendix 3) and vegetative buds (Appendix 4) of cv. Seedling after 0, 10, 20, 30, 40, 50, 60 days of continuous chilling at 7.2 C. The data are expressed as percentage of the control and each value is the average of three replications.

Appendix 5.

Days at 7.2 C	Chromatogram Segments									
	1	2	3	4	5	6	7	8	9	10
0	113.4	104.5	102.0	91.1	70.9	61.2	67.2	63.8	91.0	101.6
10	103.1	102.5	93.6	87.9	90.3	66.5	66.5	69.1	69.1	93.8
20	112.6	105.1	93.9	97.9	97.7	73.5	61.3	62.6	61.0	93.5
30	94.4	94.0	93.4	87.5	74.9	58.1	56.0	58.2	63.5	93.0
40	102.3	91.7	92.5	92.2	78.6	63.2	62.4	63.7	67.1	92.3
50	99.2	94.5	83.6	65.3	67.0	62.3	62.9	62.2	81.7	87.8
60	105.6	96.7	100.2	103.5	94.4	68.3	62.5	63.9	64.4	92.8

Appendix 6.

Days at 7.2 C	Chromatogram Segments									
	1	2	3	4	5	6	7	8	9	10
0	93.3	96.7	74.7	66.2	59.0	58.8	56.8	68.0	72.4	89.4
10	106.2	95.0	87.6	71.8	65.9	63.1	61.7	65.2	62.3	89.1
20	96.1	92.1	94.4	85.9	67.4	57.6	55.2	59.5	63.8	84.3
30	103.0	91.6	91.7	60.7	54.5	53.6	55.4	58.7	73.9	87.8
40	108.9	100.9	84.6	81.3	65.7	64.3	68.4	70.4	81.2	102.8
50	95.2	99.1	103.1	97.5	68.0	60.4	61.4	57.4	64.3	90.8
60	102.5	107.4	96.6	102.4	83.0	62.9	62.9	64.7	65.9	94.4

Appendixes 5 and 6. Responses of wheat coleoptiles to endogenous growth promoters and inhibitors in the neutral/basic fraction of ether extracts from peach floral buds (Appendix 5) and vegetative buds (Appendix 6) of cv. LaGold, after 0, 10, 20, 30, 40, 50, 60 days of continuous chilling at 7.2 C. The data are expressed as percentage of the control and each value is the average of three replications.

Appendix 7.

Days at 7.2 C	Chromatogram Segments									
	1	2	3	4	5	6	7	8	9	10
0	99.7	97.5	97.9	92.5	96.1	74.5	58.2	57.4	55.6	93.5
10	94.3	94.4	96.6	82.5	87.6	56.3	53.4	58.9	64.3	89.0
20	112.5	103.7	95.2	98.2	89.5	73.0	60.9	65.9	71.4	94.0
30	86.0	85.5	85.9	76.4	56.8	55.0	54.6	54.1	84.5	91.6
40	97.2	94.4	92.1	89.8	94.9	64.9	64.9	65.7	80.8	89.2
50	101.0	92.4	69.9	60.7	60.6	60.7	62.7	77.6	92.6	91.2
60	113.5	99.8	102.4	94.6	89.1	75.1	65.3	63.2	80.0	90.9

Appendix 8.

Days at 7.2 C	Chromagogram Segments									
	1	2	3	4	5	6	7	8	9	10
0	91.3	89.8	86.6	88.6	87.4	57.5	50.4	51.2	52.0	81.5
10	114.5	108.8	92.0	98.0	85.6	66.9	66.7	69.8	82.1	94.4
20	105.0	95.9	92.0	90.9	86.0	54.5	53.1	58.4	68.8	87.6
30	97.7	100.0	99.2	98.3	61.5	58.4	58.3	58.9	70.6	95.6
40	104.4	101.9	99.8	96.8	92.2	62.5	64.5	74.0	82.7	95.3
50	103.3	107.2	105.9	108.8	79.6	66.5	69.0	66.9	66.9	99.3
60	95.6	98.7	89.2	80.3	67.5	55.2	68.9	55.7	58.8	86.4

Appendixes 7 and 8. Responses of wheat coleoptiles to endogenous growth promoters and inhibitors in the neutral/basic fraction of ether extracts from peach floral buds (Appendix 7) and vegetative buds (Appendix 8) of cv. Seedling, after 0, 10, 20, 30, 40, 50, 60 days of continuous chilling at 7.2 C. The data are expressed as percentage of control and each value is the average of three replications.

Appendix 9.

Analysis of Variance Table for Acidic Fraction of Floral and Vegetative Buds

Sources of Variation	Degrees of Freedom	Sum of Squares	Mean Squares	F Value
Block (Cultivars)	1	24.05	24.05	
Bud Types	1	451.82	451.82	0.95 NS
Period of Chilling	5	3966.87	793.37	1.66 NS
Bud X Period	5	826.50	165.30	0.35 NS
Error A	11	5245.18	476.83	
Rf	9	18672.42	2074.71	22.87 **
Bud X Rf	9	973.18	108.13	1.19 NS
Period X Rf	45	7660.17	170.23	1.88 **
Bud X Period X Rf	45	4431.43	98.48	1.09 NS
Error B	108	8599.87	79.63	
Residual	491	44535.74	90.74	
Corrected Total	719	90142.05	125.37	

Appendix 10.

Analysis of Variance Table for Neutral/Basic Fraction of Floral and Vegetative Buds

Sources of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Value
Block (Cultivars)	1	626.96	626.96	
Bud Types	1	230.42	230.42	0.21 NS
Period of Chilling	5	4343.31	868.66	0.79 NS
Bud X Period	5	7595.79	1519.16	1.37 NS
Error A	11	12169.52	1106.32	
Rf	9	156085.35	17342.82	162.56 **
Bud X Rf	9	1486.36	165.15	1.55 NS
Period X Rf	45	7400.68	164.46	1.54 *
Bud X Period X Rf	45	10691.12	237.58	2.23 **
Error B	108	15673.14	145.12	
Residual	491	52383.40	106.69	
Corrected Total	719	256516.52	356.77	

Appendix 11.

Days at 7.2 C	Chromatogram Segments									
	1	2	3	4	5	6	7	8	9	10
0	100.1	95.2	87.5	86.8	86.3	83.8	79.0	83.5	85.7	93.3
10	102.9	110.8	112.9	99.5	100.1	103.4	110.0	106.8	100.1	108.8
20	110.1	106.8	97.8	92.7	96.6	97.8	98.9	98.3	97.2	102.8
30	100.9	105.6	105.8	101.6	101.3	100.1	96.1	98.8	103.6	100.8
40	100.6	94.5	85.5	81.6	80.7	79.0	83.2	92.1	86.4	87.0

Appendix 12.

Days at 7.2 C	Chromatogram Segments									
	1	2	3	4	5	6	7	8	9	10
0	103.7	99.1	91.8	90.4	86.5	88.9	89.8	105.9	94.5	92.1
10	102.0	113.3	116.0	94.8	90.8	96.1	99.4	101.3	92.8	101.4
20	99.3	103.8	97.0	95.8	93.5	92.2	92.9	110.1	103.5	102.4
30	102.4	96.1	99.8	86.0	93.4	94.0	95.5	101.5	89.7	95.2
40	96.0	105.5	83.5	83.6	82.8	86.3	81.4	98.6	89.1	88.3

Appendixes 11 and 12. Responses of wheat coleoptiles to endogenous growth promoters and inhibitors in the acidic fraction of ether extracts from peach seeds of cv. LaGold (Appendix 11) and LaGem (Appendix 12) after 0, 10, 20, 30, 40 days of continuous chilling at 7.2 C. The data are expressed as percentage of the control and each value is the average of three replications.

Appendix 13.

Days at 7.2 C	Chromatogram Segments									
	1	2	3	4	5	6	7	8	9	10
0	92.2	98.6	97.2	95.4	92.5	97.4	102.1	97.0	107.2	101.1
10	97.0	96.3	93.7	95.4	103.5	106.6	107.0	100.7	84.9	95.9
20	99.8	97.5	100.2	99.6	104.1	97.0	103.3	98.8	92.3	100.1
30	98.8	104.9	100.6	100.6	104.5	93.0	105.0	106.1	86.5	91.4
40	110.0	100.0	99.4	106.9	106.8	116.3	108.2	103.8	96.3	100.6

Appendix 14.

Days at 7.2 C	Chromatogram Segments									
	1	2	3	4	5	6	7	8	9	10
0	93.3	101.8	97.9	99.1	96.5	94.2	104.2	97.8	105.9	94.1
10	104.1	99.1	99.6	99.6	107.5	102.0	107.8	111.9	93.3	97.7
20	99.7	102.3	103.2	105.0	111.3	104.3	103.6	100.7	96.0	97.4
30	102.7	105.1	94.3	99.0	93.9	101.5	113.1	103.8	94.6	99.5
40	98.2	98.9	95.6	91.0	95.9	101.7	101.9	103.4	96.3	94.8

Appendixes 13 and 14. Responses of wheat coleoptiles to endogenous growth promoters and inhibitors in the neutral/basic fraction of ether extracts from peach seeds of cv. LaGold (Appendix 13) and LaGem (Appendix 14), after 0, 10, 20, 30, 40 days of continuous chilling at 7.2 C. The data are expressed as percentage of the control and each value is the average of three replications.

Appendix 15.

Analysis of Variance Table for Acidic Fraction of Floral Bud and Seed of cv. LaGold

Sources of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Value
Organ Types	1	1241.64	1241.64	6.08 **
Period of Chilling	4	3752.54	938.14	4.59 **
Organ X Period	4	5719.62	1429.91	7.00 **
Error A	20	4086.59	204.33	
Rf	9	4982.18	553.58	12.14 **
Organ X Rf	9	391.91	43.55	0.96 NS
Period X Rf	36	2280.66	63.35	1.39 NS
Organ X Period X Rf	36	2804.67	77.91	1.71 *
Residual	180	8207.12	45.60	
Corrected Total	299	33466.92	111.93	

Appendix 16

Analysis of Variance Table for Neutral/Basic Fraction of Floral Bud and Seed of cv. LaGold

Sources of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Value
Organ Types	1	21698.13	21698.13	89.72 **
Period of Chilling	4	869.91	217.48	0.90 NS
Organ X Period	4	1923.47	480.87	1.99 NS
Error A	20	4836.85	241.84	
Rf	9	16700.53	1855.62	36.40 **
Organ X Rf	9	21376.36	2375.15	46.60 **
Period X Rf	36	4993.66	138.71	2.72 **
Organ X Period X Rf	36	1836.60	51.02	1.00 NS
Residual	180	9175.30	50.97	
Corrected Total	299	83410.80	278.97	

Appendix 17.

Days at 7.2 C	Chromatogram Segments									
	1	2	3	4	5	6	7	8	9	10
0	103.8	106.3	83.8	100.0	87.6	87.6	93.8	108.5	85.4	78.1
60	108.9	101.4	93.6	95.2	79.7	87.9	91.4	100.1	93.0	90.7

Appendix 18.

Days at 7.2 C	Chromatogram Segments									
	1	2	3	4	5	6	7	8	9	10
0	90.6	95.6	91.8	98.4	95.7	89.3	96.9	86.7	69.5	76.3
60	97.4	100.7	108.3	98.4	96.7	99.7	89.1	84.5	66.0	75.0

Appendixes 17 and 18. Responses of wheat coleoptiles to endogenous growth promoters and inhibitors in the acidic fraction (Appendix 17) and the neutral/basic fraction (Appendix 18), of ether extracts of bud scales of pecan, cv. Desirable after 0 and 60 days of continuous chilling at 7.2 C. The data are expressed as percentage of the control and each value is the average of three replications.

AUTOBIOGRAPHY

Charn Lum Loh was born on August 14, 1934 in Kuala Lumpur, Malaysia. He completed his secondary education at the Victoria Institution, Kuala Lumpur in 1953, after which he attended the College of Agriculture, Serdang, graduating with a diploma in Tropical Agriculture in 1957. He then worked as an Agricultural Assistant at the Federal Experiment Station, Department of Agriculture, Serdang, for ten months before being awarded a Colombo Plan Scholarship to further his studies at Lincoln College, New Zealand, from which he received his B. Agr. Sc. (Hort.) in 1961 and the M. Hort. Sc. in 1963.

He then returned in 1964 to the Federal Experiment Station, Serdang and accepted a position as an Agronomist until he was selected to study in the United States under the Fulbright-Hays Program in 1968. He registered as a graduate student in the Ph.D. program in the Department of Horticulture, Louisiana State University, Baton Rouge.

In 1966 he married the former Pamela Sodhy and they have a son Richard Keng Yan and a daughter, Maria Cheng Yee.

EXAMINATION AND THESIS REPORT

Candidate: Charn Lum Loh

Major Field: Horticulture

Title of Thesis: Endogenous Growth Promoters and Inhibitors in the Regulation of Rest in the Floral Bud, Vegetative Bud, and Seed of Prunus persica

Approved:

C. W. Porter Jr
Major Professor and Chairman

Max Goodrich
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Date of Examination:

May 8, 1972